New mesopelagic larvaceans in the genus *Fritillaria* from Monterey Bay, California

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Three new species of *Fritillaria* are described from specimens collected by a remotely operated vehicle (ROV) between 180 and 735 m depth in Monterey Bay, California. *Fritillaria rex* becomes the largest species now described for this genus (trunk length up to 10 mm, tail length up to 18 mm). This species is characterized by five or six narrow muscle bundles on each side of the tail, slit-shaped spiracles, a spherical ovary and a cylindrical testis. *Fritillaria amphigonadis* (trunk length up to 5.2 mm, tail length up to 7.5 mm) is characterized by two narrow muscle bundles on each side of the tail, slit-shaped spiracles, paired spherical ovaries, and a unique pi-shaped testis. *Fritillaria lucifer* (trunk length up to 4.1 mm, tail length up to 7.0 mm) has 12 extremely thin muscle bundles distributed broadly across the tail, rounded spiracles, a spherical ovary and a U-shaped testis. An additional mesopelagic *Fritillaria* appears to be consistent with the description of the Mediterranean *F. fagei*, but specific differences in pharyngeal cells, cellular patterns on the tail, and gonadal morphology suggest that the specimens from Monterey Bay are a new variety, *F. fagei mbarii*. Based on the relatively limited number of collections (i.e. only 20 specimens yielding four unique taxa), it would appear that the possible diversity of larvaceans that live below the surface mixed layer is significantly underestimated.

INTRODUCTION

With the increased utilization of manned and robotic submersible vehicles in the past two decades our knowledge of soft-bodied zooplankton has increased substantially (e.g. Hamner & Robison, 1992; Mills, 1995; Robison et al., 1998; Silguero & Robison, 2000; Raskoff, 2002). Many such animals (e.g. ctenophores, larvaceans, medusae, siphonophores) are too fragile to survive collection with traditional plankton nets and can only be obtained intact by *in situ* techniques (e.g. Hamner et al., 1975; Harbison, 1983; Youngbluth et al., 1990; Fenaux, 1992). Despite their fragility, soft-bodied zooplankton are important components of marine zooplankton both as herbivores and predators. The filter-feeding larvaceans (=appendicularians), for example, are often the second or third most abundant group in zooplankton samples (e.g. Hopcroft & Roff, 1998; Gorsky & Fenaux, 1998). The majority of new larvacean species described in recent decades have been collected, primarily with submersibles (Fenaux & Youngbluth, 1990, 1991; Fenaux, 1992, 1993; Hopcroft & Robison, 1999), rather than by nets (Flood,

2000). As with their near-surface counterparts, 'new' mesopelagic species may be surprisingly common (Hopcroft, 2004; B.H. Robison, unpublished data).

Fritillaria is the most speciose genus within the order (Fenaux, 1998) and therefore might be expected to contain the largest number of species awaiting discovery. Nonetheless, nine new species have been added to the family Oikopleuridae in the past two decades, while no species have been added to the family Fritillariidae. This pattern occurs because fritillariids are generally much smaller than oikopleurids, and therefore more difficult to detect with ROVs or submersibles. Here, three new mesopelagic *Fritillaria*, *F. rex*, *F. amphigonadis* and *F. lucifer*, are described from Monterey Bay, California. Morphological observations of the co-occurring mesopelagic *F. fagei*, designated as a new variety *mbarii*, are also presented.

MATERIALS AND METHODS

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
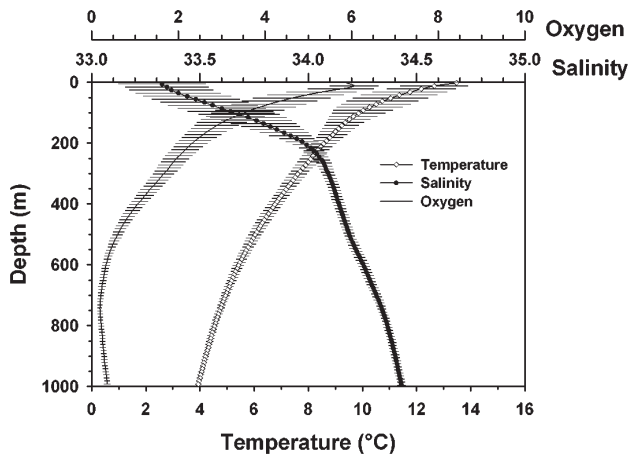
Figure 1. Average temperature, salinity and oxygen profiles for the upper 1000 m at the site of sample collection based on five years of weekly measurements from January 1989 to December 1994. Standard deviations for data set are indicated.

Monterey Submarine Canyon. Most specimens were obtained during 1997 and 1998 between ~180 and 735 m depth, where temperature typically ranges between 4 and 9°C (Figure 1). All larvaceans were collected with 'detritus' samplers (Youngbluth, 1984). Descriptions are based on observations of living specimens, or on specimens pacified by the addition of several drops of formalin to stop tail movement. Detailed drawings were made concurrently using a camera lucida. Where possible, measurements were obtained from these drawings because specimens can undergo significant shrinkage (~20–25%) and some distortion after long-term preservation, greatly complicating the interpretation of morphological features. Descriptions are based on 13 specimens of *Fritillaria rex*, 5 specimens of *F. amphigonadis*, and 2 specimens each of *F. lucifer* and *F. fagei mbarii* (Table 1). Type material has been deposited at the California Academy of Sciences (*F. rex* CASIZ 170743–170748, *F. amphigonadis* CASIZ 170961–170962, *F. lucifer* CASIZ 170958–170959, *F. fagei mbarii* CASIZ 170960). Drawings represent composite syntheses of these specimens. A more detailed description of form and function is provided for *F. rex*. The larger size of this species allowed observation of structures not easily resolved in smaller species within this family.

In situ observations were made concurrent with these collections, but camera magnification and resolution allowed identification only to the generic level and precluded useful still image capture from that period. Video sequences and frame-grabs collected by 'Ventana' at the same station from 2000 to present using a High Definition camera, plus video and still images from the ROV 'Tiburon' collected at a more

offshore station in 3500 m of water, were subsequently reviewed. Close-up images from this later period are of sufficient quality to resolve features allowing species level identification.

SYSTEMATICS

Order LARVACEA, APPENDICULARIA
or COPELATA
Family FRITILLARIIDAE Lohmann 1915
Genus *Fritillaria* Fol 1872
Fritillaria rex sp. nov.
(Figure 2)

Description

Trunk

In dorsal view the trunk is an elongate cylinder, slightly 'dumb-bell' in shape, being widest anteriorly. As is typical of fritillariids the epidermis lacks distinct cells, but cell nuclei (likely equivalent to Lohmann's nettle-cells) are regularly scattered across this tissue. As is also characteristic, the anterior end is modified by an expanded and encircling fold of tissue called the hood. This feature envelops the anterior end, forming a tightly closed vestibule that protects the house-forming oikoplastic tissue. Anteriorly, a broadly rounded rostrum (or upper lip) projects forward through the hood, that is covered with more closely spaced cell nuclei than occurs elsewhere on the trunk. Small horns (easily damaged and thought to assist in anchoring the trunk into the filtering house) project backward from near the mid-dorsal edge of each of the two posterior lobes. The posterior ventral surface is relatively flat, with six distinct cells arranged in a half circle. The trunk ranged in length from 4.2 to 9.8 mm (including the rostrum, but excluding the horns) and in width from 1.3 to 2.6 mm (Table 1). In lateral view, the rostrum projects anteriorly from beneath the hood, then slopes backward until reaching the narrow lower lip, which projects forward as a flattened triangular process. The maximum trunk height occurred in the pharyngeal region and ranged from 1.0 to 2.5 mm.

Ventrally, the hood meets medially as two broad and closely applied lobes. Anteriorly, these lobes are closely applied to the rostrum. Posteriorly, they sweep outward to expose the shallow common vestibule into which each of the rounded external spiracular lumens open mediolaterally. The hood continues along the outer lateral edge of each external spiracular lumen, into a tubular groove that extends from the hood vestibule posteriorly to a distinct and enlarged cell located lateral to the midpoint of each spiracle. A similar but less distinct tube occurs on the ventral midline

between the spiracles, and terminates with two smaller cells each lateral to the midline and slightly anterior to the position of the larger more lateral cells. All four cells likely represent extensions of the oikoplastic epithelium rather than serving as unique glands.

Pharyngeal region. The mouth originates sub-terminally below the rostrum, and is lined by a border of stiff papillae (likely fused cilia) ~5–6 times as long as broad. The overall shape of the mouth resembles a centrally constricted oval in dorsal view. The buccal cavity constricts laterally, and expands dorsally before being encircled by the ciliated peripharyngeal bands. The spacing of cell nuclei in the buccal cavity remains similar to that of the rostrum but decreases several-fold beyond the peripharyngeal bands in the pharyngeal cavity. The peripharyngeal bands begin on the dorsal

quarter of the endostyle, loop around the inner margin of the pharyngeal cavity, and then rejoin dorsally, extending for a short distance posteriorly before ending as a thick, blunt lobe. A ciliated ridge exists midventrally along a ridge on the floor of the pharynx and extends to ~75% of the spiracle's length before ending. These ridges typically suspend and transport the mucilaginous pharyngeal feeding filter produced by the endostyle.

The endostyle is crescent-shaped in lateral view, broadly expanded in dorsal view at its anterior end, and lies approximately midway between the mouth and the spiracles. The pair of large elongate ciliated spiracles, that pull water through the pharynx, sit recessed approximately midway in the floor of the expanded pharynx, appearing slit-shaped in dorsal view and semi-circular in lateral view. Below the spir-
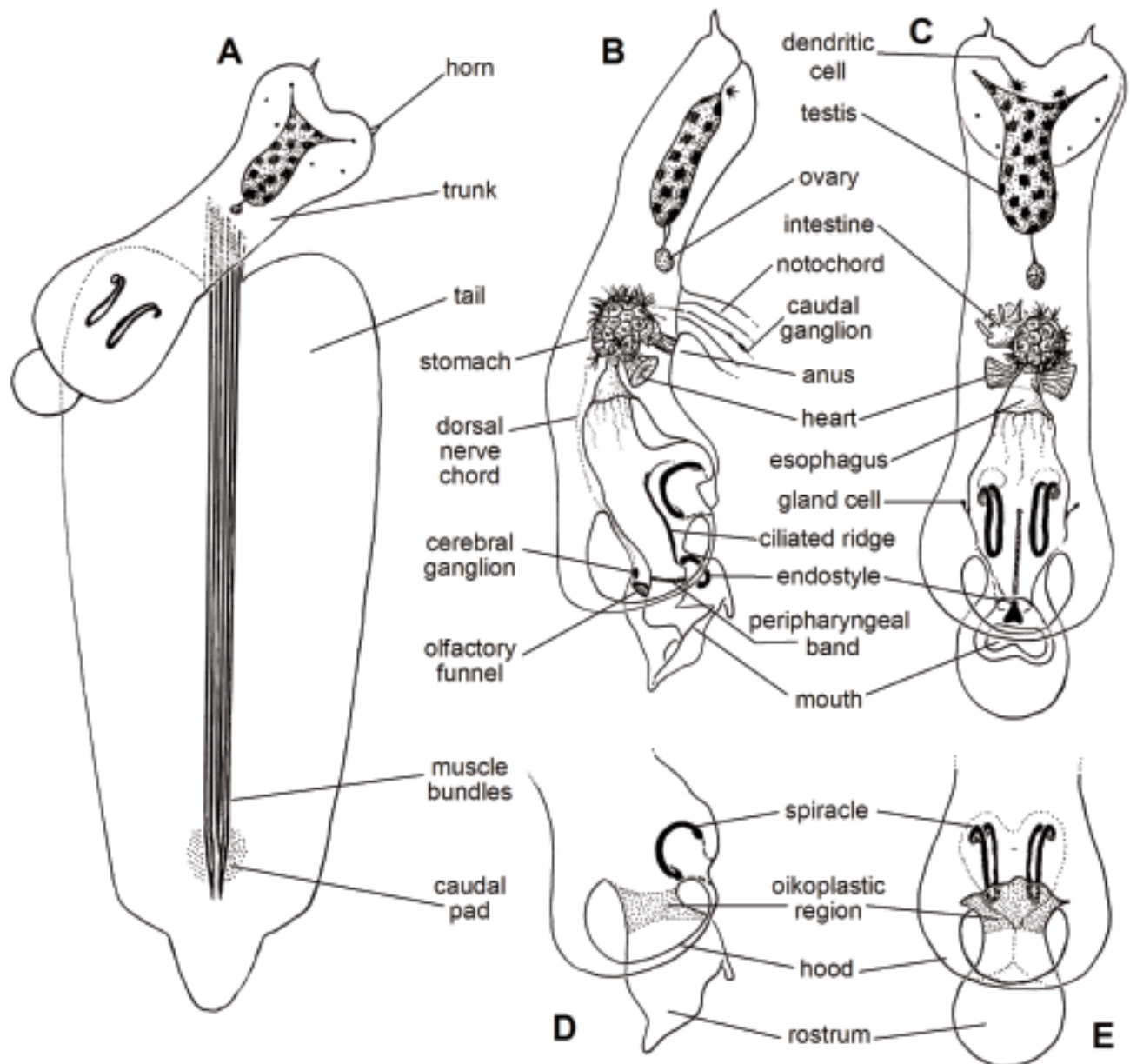

Figure 2. Composite drawing of *Fritillaria rex*. (A) Whole animal; (B) lateral view of trunk;. (C) dorsal view of trunk; (D) lateral view; and (E) dorsal view of anterior trunk illustrating extent of oikoplastic region.

acles, their lumens narrow to roughly circular cross-sections, and cell nuclei lining the lumen become numerous. Immediately behind the spiracles, the pharynx constricts laterally, and four longer, ciliated tracts begin mid-ventrally, mid-dorsally and mid-laterally that extend to the opening of the oesophagus. Four additional tracks occur between the longer tracks but are less than half the length of the longer tracks.

Digestive region. The ciliated oesophagus is funnel-shaped and constricts to a pronounced sphincter valve as it meets the anterodorsal edge of the stomach on the sagittal plane of the body. Viewed dorsally, the globular stomach lies principally on the left side of the animal. The stomach consists of a relatively small number of large polygonal cells with 6–10 tufts of 5–8 papillae clustered along an indistinct ridge. Two groups of tufts are located anterodorsally, with the remainder situated more laterally, posteriorly and ventrally. The short intestine arises horizontally from the right side of the stomach, widening slightly before either one digitate or three bulbous processes (variably called pyloric glands or glandular appendages in the literature) appear on each side of the intestine, then the intestine turns downward into the rectum. The anus opens to the right of the sagittal plane, slightly forward of the tail. Several other rounded processes bud off from the intestine and rectum. It is notable that the digitate processes on the stomach appear to be solid, while those of the intestine appear to be hollow.

Genital region. The genital system of this protandrous species was observed in various phases of maturity. In less mature specimens, an ellipsoid ovary of variable size was suspended by connective tissue between the stomach and the larger elongate sac-shaped testis that occupied 20–25% of the length of the trunk. Posteriorly, the testis appears connected to the body wall by tissue (possibly sperm ducts) that attach to the most posterior of the six epidermal cells on the outer side of the trunk. In more mature specimens, the testis had liberated its sperm and was reduced to an empty sac of variable size, while the ovary was enlarged and became elongated as it shifted more posteriorly into

Table 1. *Mesopelagic* Fritillaria *species collected by the ROV 'Ventana' in Monterey Bay. Asterisk indicates measurements were obtained from preserved material, and increased by 25% to account for the shrinkage determined by three* F. rex *specimens measured both live and after long-term preservation.*

Species	Depth	Date		Tail			Trunk	
				Length	Width	Depth	Length	Width
F. rex	363	07/02/1991	*	6.25	–	–	13.63	–
F. rex	506	22/08/1991	*	8.38	2.31	2.34	13.90	6.03
F. rex	735	28/01/1998	*	7.55	2.16	2.13	16.15	6.01
F. rex	312	29/05/1998		8.36	2.64	2.00	16.36	7.00
F. rex	326	29/05/1998		6.89	2.17	1.67	12.50	4.94
F. rex	392	09/06/1998		8.06	2.17	2.17	15.28	7.28
F. rex	405	12/06/1998	*	8.39	2.25	2.34	16.40	5.65
F. rex	511	30/07/1998		8.37	2.07	2.03	15.18	7.18
F. rex	389	03/11/1998		8.14	2.58	2.20	14.56	6.39
F. rex	398	29/12/1998	*	8.13	2.21	2.43	17.43	7.24
F. rex	559	29/12/1998	*	9.78	2.65	2.45	18.16	6.11
F. rex	475	29/12/1998	*	7.54	2.15	2.00	–	–
F. rex		no label	*	4.23	1.28	1.00	10.66	–
F. amphigonadis	255	30/07/1998		4.84	1.09	0.87	7.12	3.32
F. amphigonadis	192	31/07/1998		4.10	1.09	0.82	6.51	2.95
F. amphigonadis	179	10/09/1998		3.57	0.82	0.75	6.39	2.50
F. amphigonadis	189	11/09/1998		5.20	1.33	1.05	7.52	3.43
F. amphigonadis	181	30/09/1998		2.83	–	–	5.59	–
F. lucifer	332	16/07/1997		4.08	1.17	1.34	7.00	2.50
F. lucifer	373	29/05/1998		2.83	0.89	0.89	5.22	2.17
F. fagei	305	29/09/1997	*	4.23	1.28	1.00	10.66	–
F. fagei	261	30/09/1998		4.41	1.33	1.41	10.83	3.89

some of the space vacated by the testis. Immediately behind the testis is a pair of flattened transparent cells with numerous dendritic processes.

Nervous system. The cerebral ganglion and associated spherical statocyst lie dorsally on the sagittal plane just above the junction of the peripharyngeal bands. A prominent ciliated olfactory funnel that connects into the buccal cavity precedes the ganglion. Cerebral nerves were not identifiable. The main nerve chord leaves the cerebral ganglion travelling dorsally, passing over the junction of the stomach and intestine, and then downward toward the tail. The nerve chord enters the tail medially, then turns to the left as it enters the tail along the lateral edge of the notochord. The nerve cord forms a visible caudal ganglion against the notochord prior to the expansion of the tail's fins. The caudal ganglion is similar in size to the cerebral ganglion with numerous small nerves leaving the ganglion and innervating the caudal muscles. The caudal nerve can be traced to the end of the tail muscles, suspended along the left edge of the notochord. A series of nine small ganglia appear along the length of the caudal nerve, which innervate the caudal musculature.

Heart. The heart is located ventrally, beneath the oesophagus and forward of the stomach, stretching transversely more than half the trunk's width. The heart is roughly tubular and on each end there are two large (smooth muscle) cells that connect dorsally to six striated muscles, and ventrally by a less mobile surface that contains two cells medially, similar to those at the ends but much less obvious. Peristaltic contractions of the muscles pump fluid through the heart and down one of the vascular sinuses of the tail, while return flow moves up the lumen on the opposite side of the tail.

Oikoplastic layer. As in all fritillariids, the oikoplastic region is confined to a band beneath the hood that encircles the pharynx posterior to the endostyle and overlaps the anterior end of the spiracles. The oikoplastic region is expanded and highly sculptured by an intricate arrangement of specialized cells on the dorsal surface, and ends where the hood begins to curl forward. Compared to the oikopleurids, this region is greatly reduced and the cell groups forming the various parts of the house are difficult to identify (Flood, 2003).

Tail

The tail is broad, being 40–50% of its length at the widest point. The length is twice that of the trunk. Like the trunk, the tail epidermis lacks distinct cells,

but nuclei may be arranged in distinct rows running slightly oblique to the transverse plane. The tail begins in the mid-ventral trunk just behind the stomach, being ~3/4 of the trunk in width at its origin. After about one trunk width in distance, the fin of the tail begins, its 'shoulders' expanding laterally and somewhat proximally to full width. The tail then tapers slightly until level with the end of the notochord, where it narrows abruptly to less than half its width and becomes broadly acuminate terminally.

The notochord begins at the tail's insertion to the trunk and runs most of the length of the tail with a vascular sinus located laterally on each side. The tail muscles do not begin until slightly below this point, and arise as five or six distinct muscle bundles on each side of the tail and run most of the tail's length. Ten large branching nuclei for the muscle cells are spaced regularly along the midline on each side of the tail. In general, the total width of the muscular area corresponds to the width of the underlying notochord and associated vascular sinuses. Distally, the muscles on each side of the tail begin to narrow and move medially. When six muscle bundles are present, either as the muscles narrow the two medial bundles may first join into a single bundle, then join more distally to one of the more lateral muscle bundles; or each medial bundle may join with bundle lateral to it. The remaining four muscle bundles continue to narrow and converge as they travel distally, with each lateral pair either joining (leaving only two bundles on each side of the tail) or remaining distinct but almost touching. The remaining muscle bundles end at the same point as the notochord and its sinuses, level with the narrowing of the tail fin.

Two distinct, kidney-shaped regions with larger and more numerous cell nuclei appear on only the anterior surface of the tail, overlying the area where the muscle bundles in the tail terminate. The cells appear to be arranged in distinct parallel lines, inclined slightly toward the proximal end of the tail. The epidermis in this region also appears 'rougher' than the surrounding tail surface. Technically, these could be referred to as amphichordal cells like any other symmetrically arranged structures in the tail, however, due to the large number of cells involved (i.e. >50), and the recurrence of similar features in other species described subsequently, we shall refer to these features as 'caudal pads'.

Tail length varied from 10.7 to 18.2 mm (Table 1). The outer, non-muscular margins of the tail are relatively fragile and undergo considerable shrinkage and distortion during preservation. This shrinkage alters the appearance of the muscle bundles, narrows the apparent width of the tail, and often masks the termi-

nal, nearly tri-lobed shape of its distal end. These distortions contribute to high variability in the ratios from tail morphometrics when measurements are made from preserved specimens (Table 1).

House

The house is completely consistent with the laboratory based observations of *Fritillaria borealis* (Flood & Deibel, 1998; Flood, 2003). The house (Figure 3) consists of two symmetrical food concentrating filters, with their anterior surfaces distinctly scalloped. There is a diffuse outer sphere that envelops the animal plus the obvious food concentrating filter that is not noted from laboratory observations. Movement of the tail appears to be required to keep the house inflated, otherwise it collapses into a tight ball. In one instance an animal was observed to repeatedly inflate and deflate the house. Undisturbed animals are periodically encountered without a house, but we lack data to establish how common such an occurrence is, and how long such events last.

Etymology

The specific name *rex* refers to this species being a 'king' for this group, in terms of size and prevalence in mesopelagic waters.

Synonymies

The species bears many similarities to the currently accepted description of *Fritillaria aberrans* Lohmann, 1896 as redescribed by Tokioka (1958), but even greater similarity to the now discounted *F. magna* (Lohmann, 1896). Lohmann's original description of both species is based on only a few specimens collected in the northern and equatorial Atlantic Ocean, and although each species is described in some detail, only the digestive systems were illustrated at that time. Both appear on Lohmann's species lists in subsequent expeditions. Additional, and still incomplete, anatomical information does not appear until a comparative review (Lohmann, 1933), where details on tail musculature are presented. All type material was later destroyed during World War II. Tokioka (1958), unhappy with the lack of specificity in Lohmann's species, and referring to 49 specimens of variable quality collected from the Pacific Ocean, considered *F. aberrans* and *F. magna* to be synonymous, and designated *F. aberrans* as taking precedence.

We might have designed this species as a resurrection of *F. magna* were the initial descriptions more complete, were type material of that species available for examination, or were suitable material from the Atlantic type localities available. For now we are inclined to consider *F. magna* as *nomen nudum*. The presence of our specimens in a different ocean, plus significant discrepancies in the shape of the tail (acuminate in *F. magna*, nearly trilobed in *F. rex*), and the shape of the cells on the stomach (simply spherical in *F. magna*, numerous digitate process per cell in *F. rex*) lead us to erect a new species. We accept that some of these differences may arise as preservation artefacts, but given the general detail of Lohmann's observations, we consider these differences to be real. Future collections from the Atlantic, and molecular characterization of specimens, may ultimately shed light on the appropriateness of this decision.

Diagnoses

Fritillaria rex is readily separated from all other accepted *Fritillaria* species except for *F. aberrans* and *F. lucifer* by the presence of a tail musculature separated into several distinct bundles. It is distinguished from *F. aberrans*, which has 10–12 muscles bundles on each side of the tail, by having only five or six muscle bundles per side. Secondarily, *F. aberrans* is characterized by having a trunk that is truncated or acuminate posteriorly, and a tail that is broadly and simply acuminate. *Fritillaria rex* differs from *F. lucifer* by having a tail musculature that is restricted to overlying the notochord and vascular sinuses, rather then distributed broadly across the tail. Additionally, *F. rex* has slit-shaped rather then round spiracles as in *F. lucifer*. The testis and trunk are linear in *F. rex* but bifurcated in *F. lucifer*. Finally, there is a notable difference in size between *F. rex* and most other *Fritillaria* species.

It is of relevance at this point to contrast Tokioka's (1958) re-description of the closely related *F. aberrans* to that of *F. rex*. Tokioka considers *F. aberrans* to be characterized by: a posterior margin of the trunk that is generally truncated, or rarely forming a pointed end; elongate (but flattened) spiracles; spherical cells protruding from the stomach; a tail musculature of 10–12 bundles per side; and only a small pair of glandular cells at the distal end of the acuminate tail. We find *F. rex* to be characterized by: an expanded and slightly incised posterior margin to the trunk; elongate and extremely arched spiracles; cells protruding from the stomach with numerous digitate processes; a tail musculature of five or six bundles per side; and an obvious caudal pad on a nearly trilobed tail that lacks small glandular cells terminally. Tokioka described a number of glands present within the trunk of *F. aberrans*: a pair of large roundish glands behind the endostyle and level with the anterior end of the spiracles (his gland-cell 1), a pair of small gland cells posterior to this pair (gland-cell 2), a medium set lateral to the middle of the spiracles (gland-cell 3), and an elongate set lateral to
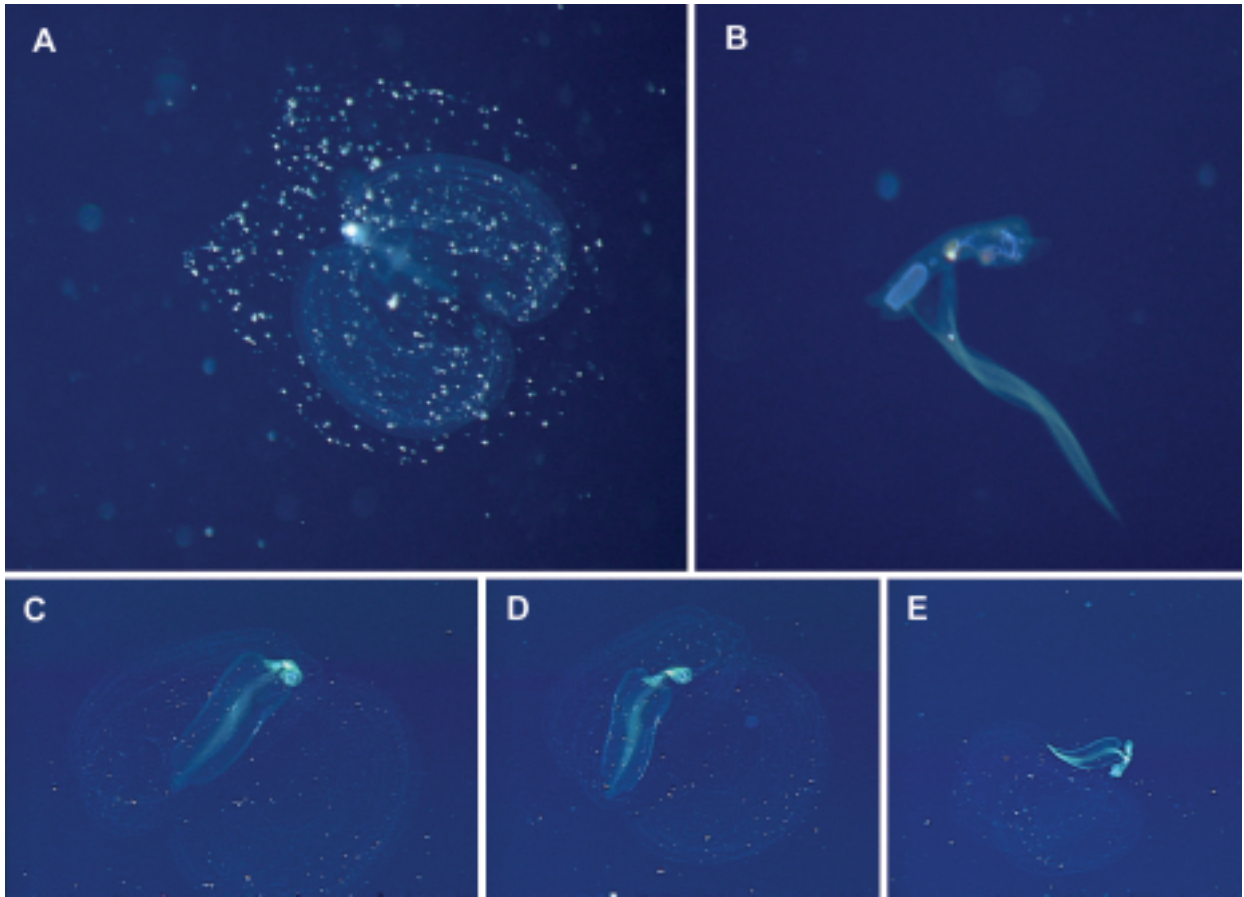
Figure 3. *In situ* images of *Fritillaria rex*. (A) Ventral view of *F. rex* inside its house indicating two symmetrical food concentrating filters. Bright white circle is located within animal's trunk; (B) free swimming *F. rex*; (C&D) posterior view of *F. rex* and house; (E) dorsolateral view of *F. rex* and house.

the middle of the testis (gland-cell 4). We find structures in *F. rex* (proposed as extensions to the oikoplastic epithelium) that can be related to gland-cell 2 and 3, but no trace of anything at the locations of gland-cell 1 or gland-cell 4.

Tokioka makes no specific mention of cell nuclei on the surface of the trunk or tail of *F. aberrans* (which presumably would have been noticed given his observations of gland cells), while we find these nuclei readily apparent and numerous in *F. rex*. Tokioka is quite specific on the existence of a circular muscle in *F. aberrans* that encircles the pharynx, level with the posterior half of the endostyle that is distinct from the peripharyngeal band, while we find no such structure in *F. rex*. Tokioka's largest reported specimen of *F. aberrans* had a (preserved) trunk length of 6.2 mm and a tail length of 12.5 mm, although the majority of his specimens appear to have been below 5 mm trunk length and 9 mm tail length; most of our specimens are significantly larger (see Table 1). In summary, although substantial intraspecific variation is know in *Fritillaria* (e.g. Esnal et al., 1996), there are numerous and significant differences between *F. aberrans* and *F. rex* that we believe exceed such limits.

Fritillaria amphigonadis sp. nov.
(Figure 4)

Trunk

In dorsal view the trunk is an elongate cylinder, expanded slightly at the hood, over the ovaries and more so over the posterior end of the testis. A rounded rostrum projects forward through the hood. The mid-dorsal edge of each of the two posterior lobes is broadly pointed. In lateral view, the rostrum projects anteriorly from beneath the hood, then slopes backward without a notable lower lip. The maximum trunk height occurs in the pharyngeal region. On the posterior ventral surface, beneath the middle of the testis, a rounded process occurs with two distinct cells or glands, after which the trunk slopes toward its posterodorsal surface. For the specimens collected, the trunk ranged in length from 2.8 to 5.2 mm (including the rostrum), in width from 0.8 to 1.3 mm, and in height from 0.7 to 1.1 mm (Table 1).

Pharyngeal region. The mouth originates sub-terminally below the rostrum, and is relatively V-shaped in dor-
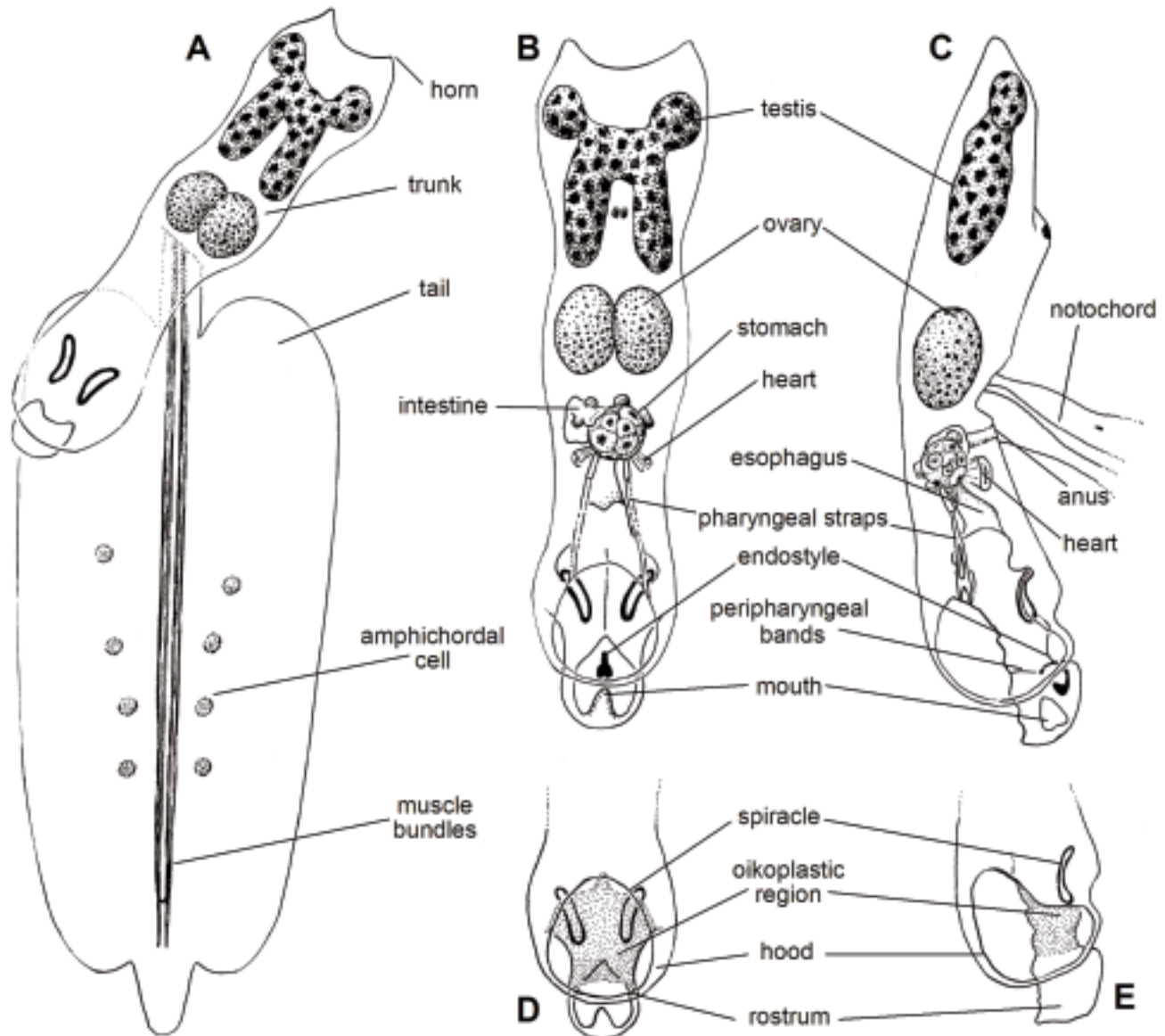
Figure 4. Composite drawing of *Fritillaria amphigonadis*. (A) Whole animal; (B) dorsal view of trunk; (C) lateral view of trunk; (D) dorsal view; and (E) lateral view of anterior trunk illustrating extent of oikoplastic region.

sal view. The mouth is lined by a border of long, stiff papillae (i.e. 8–10 times as long as wide). The buccal cavity expands, then constricts as it passes through the peripharyngeal bands, with both the mid-dorsal and mid-ventral ciliated ridges being obvious within the pharynx. The endostyle is crescent-shaped in lateral view, and broadly expanded at its anterior end in dorsal view. The pair of large elongate ciliated spiracles are recessed approximately midway in the floor of the expanded pharynx, appearing slot-shaped in dorsal view and gently curved in lateral view. The pharynx narrows behind the spiracles and extends to the opening of the oesophagus. A pair of unique strap-like structures parallel the pharynx, beginning on each

side of the stomach just above the oesophagus, then split into two bands that rejoin shortly before connecting at the posterolateral margin of the hood's vestibule. In an attempt to attribute some function to these structures, we speculate that these straps may function as retractor muscles to open the hood during expansion of a house rudiment.

Digestive region. The funnel-shaped oesophagus joins the mid-anterior surface of the stomach. Viewed dorsally, the globular stomach lies slightly to the left-hand side of the animal. The stomach is covered by a 6–8 bulbous processes, not arranged in a discernable pattern. The short intestine arises horizontally from the right side of

the stomach, widening slightly before the appearance of two bulbous glandular appendages, then turns downward into the rectum, with the anus opening to the right of the sagittal plane, slightly forward of the tail. Several additional bulbous structures or cells appear along the descending intestine and rectum.

Genital region. A pair of ellipsoid ovaries occur immediately behind the insertion of the tail. When the ovaries are small, a distinct gap occurs between them, but as the ovaries enlarge they begin to touch. The ovaries are distinctly separated from the π-shaped testis. The two anterior projections of the testis are longer and cylindrical in section, they are joined at right angles by an equally robust connective tube. At the posterolateral margins, two spherical extensions arise.

Nervous system, heart and oikoplastic layer. These are consistent with the generalities of this genus, without any remarkable variations.

Tail

The tail ranged from 5.6 to 7.5 mm in length being about 40–50% of its length at its widest point; its length about 1.5 to 2 times that of the trunk. The tail begins just behind the stomach. After about one trunk width in distance, the tail's shoulders expand laterally and somewhat proximally to full width. The tail fin then tapers only slightly until level with the end of the notochord, where it narrows abruptly forming two rounded lobes, then becomes broadly acuminate terminally.

The notochord and vascular sinuses start at the tail's insertion to the trunk and run most of the length of the tail, with the tail muscles beginning slightly below the origin of the tail. On each side of the tail, the muscle is separated into two distinct bundles, with a gap approximately equal in width to that of the muscle bundle. The combined width of both bundles and the gap are similar to that of the notochord. The muscles extend along the tail to just past the end of the notochord, at roughly the point where the tail narrows. Eight amphichordal cells are spaced along the middle half of the tail, on its anterior surface, either along the lateral margins of tail's vascular sinuses, or displaced slightly outward into the fin. Curiously, in some specimens, as few as four cells occurred and the arrangement of the cells was not perfectly symmetrical.

Etymology

The specific name *amphigonadis* refers to the unique paired structure of the gonads on both sides of the trunk.

Synonymies

None.

Diagnoses

Fritillaria amphigonadis is easily separated from all other *Fritillaria* by its paired but joined gonadal structure, and the strap-like features beside the pharynx. This species shares some similarities with *F. charybdae* Lohmann and *F. urticans* Fol, which also have paired gonads, slot-shaped spiracles and V-shaped mouths, but differs notably from both by having a tri-lobed tail and four pairs of amphichordal cells on the tail fin. In *F. charybdae* the ovaries surround the margin of each testis, while in *F. urticans* the ovaries are attached to the testis with each aggregated ovary-plus-testis more widely separated and laterally compressed than occurs in *F. amphigonadis.*

Fritillaria lucifer sp. nov.
(Figure 5)

Trunk

The shape of the trunk deviates notably from the elongate cylinder typical of many fritillariids. The anterior end of the trunk is bulbous with a large vestibule beneath the hood. At the point where the tail originates, the trunk is constricted to less than half the width and height of the anterior section. Posterior to the insertion of the tail, the trunk re-expands to greater than the width of the anterior portion, forming two distinct lobes each ending in a pronounced horn. A rounded rostrum projects forward through the hood. In lateral view, the rostrum projects anteroventrally from beneath the hood, then slopes backward without a pronounced lower lip. The maximum height of the trunk is anterior to the spiracles. The posterior ventral surface is smoothly rounded and slopes toward the posterior dorsal surface of the trunk. For the specimens collected, the trunk ranged in length from 2.8 to 4.1 mm (including the rostrum), in width from 0.9 to 1.2 mm, and in height from 0.9 to 1.3 mm (Table 1).

Pharyngeal region. The mouth originates sub-terminally below the rostrum and is unremarkable in shape, bearing short papillae (i.e. length 4–5 times width). The buccal cavity expands, then constricts as it passes through the peripharyngeal bands. Within the pharynx there is an obvious mid-ventral ciliated ridge. The pharynx expands dorsally and widens ventrolaterally to accommodate the pair of circular spiracles that sit recessed approximately midway in the floor of the pharynx. The pharynx narrows laterally behind the
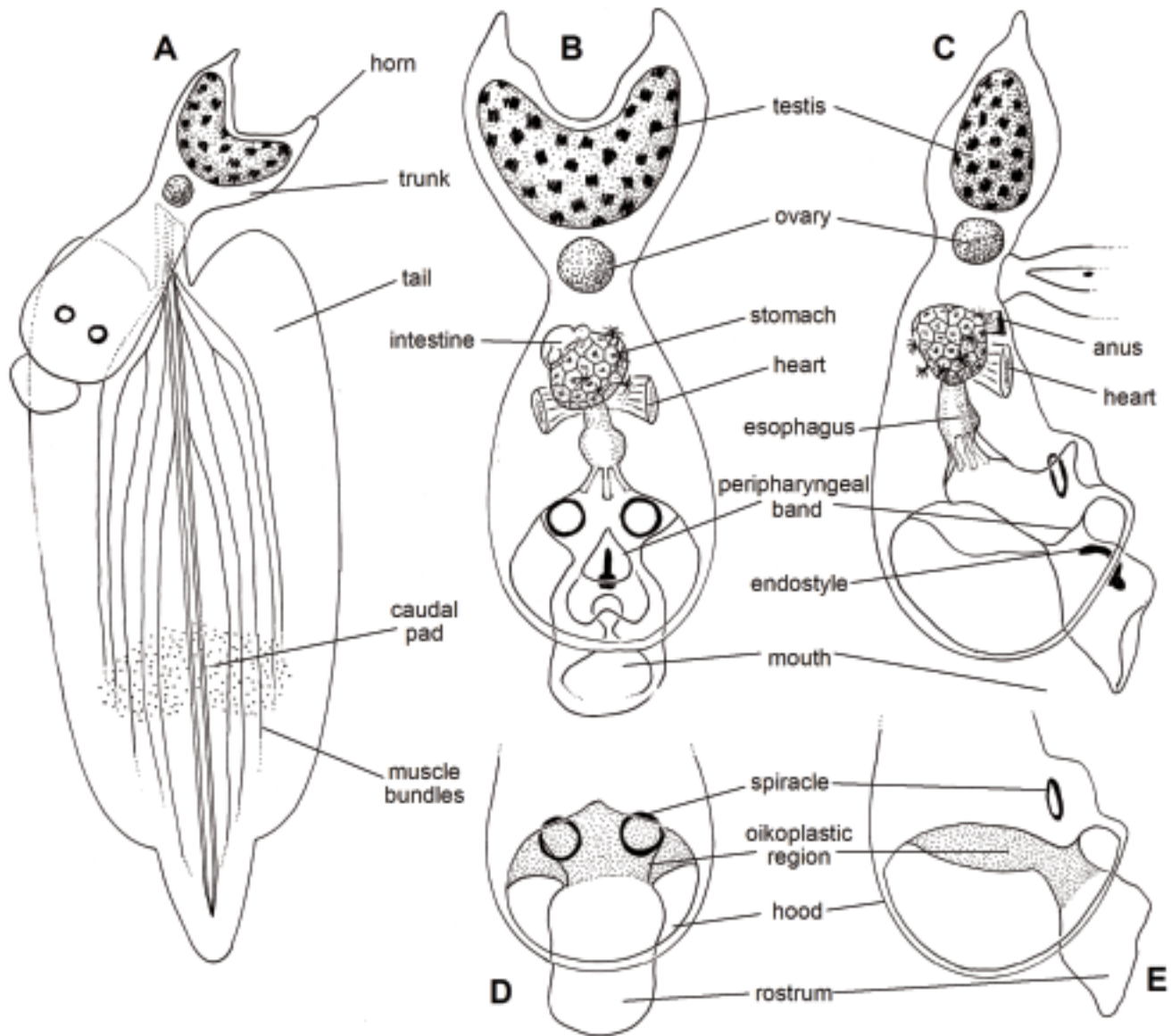
Figure 5. Composite drawing of *Fritillaria lucifer*. (A) Whole animal; (B) dorsal view of trunk; (C) lateral view of trunk; (D) dorsal view; and (E) lateral view of anterior trunk illustrating extent of oikoplastic region.

spiracles and extends to the opening of the oesophagus. Four broad ciliated fingers begin midventrally, middorsally and midlaterally and extend to the opening of the oesophagus, each being similar in length to that of the oesophagus. The endostyle is crescent-shaped in lateral view, and broadly expanded at its anterior end in dorsal view.

Digestive region. The oesophagus is somewhat spherical anteriorly, and joins the mid-anterior edge of the stomach. Viewed dorsally, the globular stomach lies on the midline (or slightly to the left side) of the trunk. The stomach has 6–8 distinct tufts of digitate papillae. The intestine is short and arises horizontally from the right side of the stomach with two bulbous glandular appendages near its origin. It turns rapidly downward

into the rectum, ending at the anus which opens slightly to the right of the sagittal plane, just forward of the tail.

Genital region. The spherical ovary occurs immediately behind the insertion of the tail. There is a gap between the ovaries and U-shaped testis. The testis is thickest anteromedially and tapers slightly posterolaterally into each lobe of the trunk.

Nervous system, heart and oikoplastic layer. These are consistent with the generalities of this genus, without any remarkable variations.

Tail

The tail ranged from 5.2 to 7.0 mm in length, with a width ~40% of length at its widest point, and its length 1.7

to 1.8 times that of the trunk. The tail begins just behind the stomach and after about one trunk width in distance, the shoulders expand laterally and proximally to near full width, continuing to expand slightly, then tapering slightly until approaching the end of the notochord, where it narrows rapidly in two smooth curves to ~30% of its width then becomes broadly acuminate terminally.

The notochord and vascular sinuses begin near the tail's insertion to the trunk, and extend the length of the tail to a point just after the major narrowing of the tail fin. The tail muscles appear below the origin of the tail, initially as six thin bundles on each side positioned over the notochord and vascular sinuses. These muscle bundles radiate outward laterally as they move distally, with one bundle bifurcating within the tail fin. Several other new bundles arise medially, distal to the origin of the tail's fin, but within the proximal quarter of the tail's length. At their maximum, 12 bundles are spread out across ~60% of the tail width, on each side of the tail. The outermost bundles end one after the other in the distal 40% of the tail's length, until only the innermost bundles remain when the tail narrows abruptly. A broad heart-shaped region of granular inclusions occupies much of the distal half of the tail's anterior surface.

Etymology
The specific name *lucifer* refers to the pronounced horns observed on the posterior part of the trunk.

Synonymies
None.

Diagnoses
Fritillaria lucifer is separated from all other *Fritillaria* by the 12 thin, branching muscle bundles that spread across the tail fin for more than half its width. The combination of a spherical ovary separated from the U-shaped testis is unique within the genus, as is the pronounced medial constriction and posterior bifurcation of the trunk.
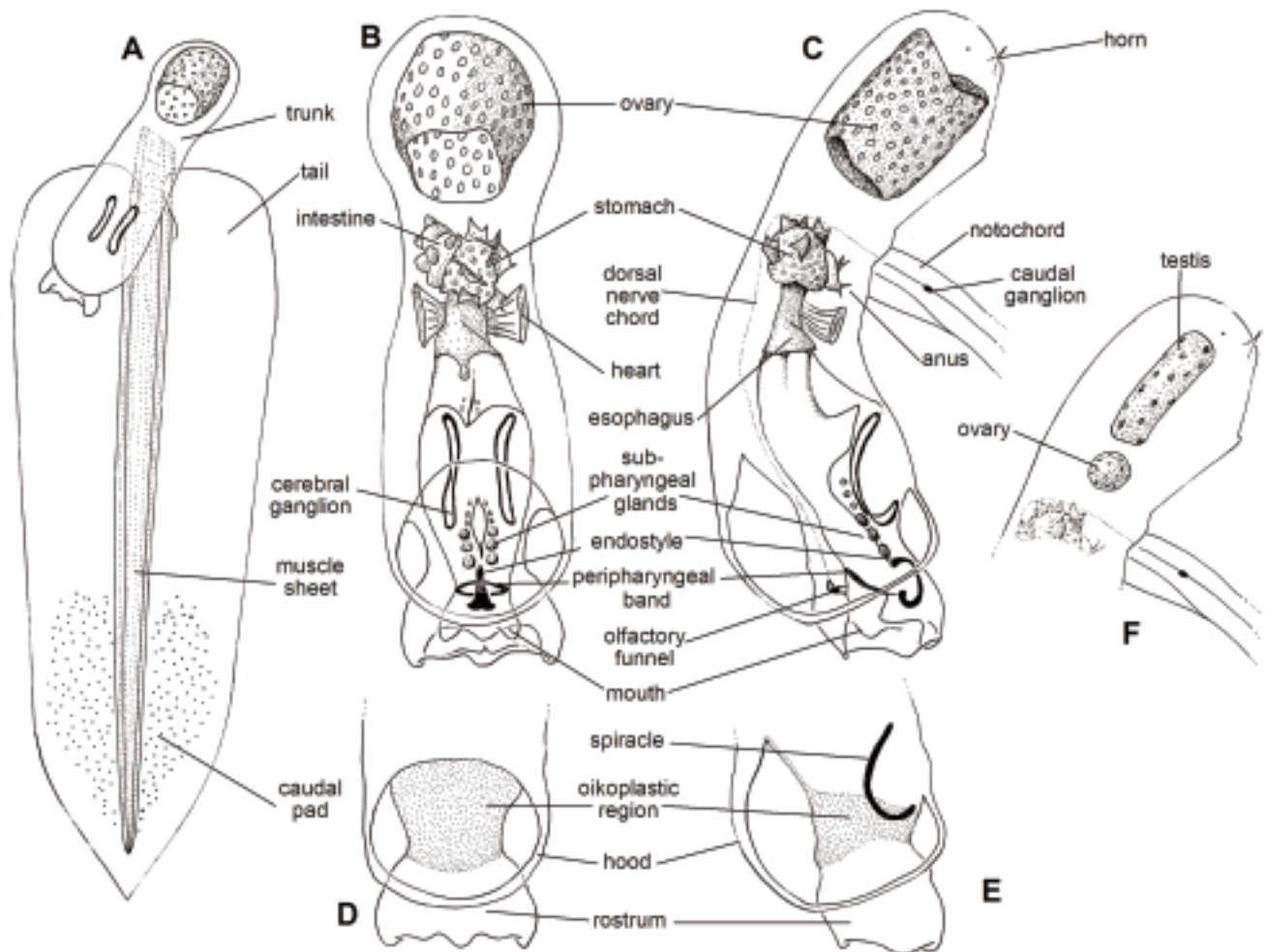

Figure 6. Composite drawing of *Fritillaria fagei mbarii* (A) Whole animal; (B) dorsal view of trunk; (C) lateral view of trunk; (D) dorsal view; and (E) lateral view of anterior trunk illustrating extent of oikoplastic region; (F) lateral view of posterior trunk on specimen with ovary and testis.

Fritillaria fagei Fenaux 1961 *mbarii* var. novo
(Figure 6)

Two specimens of this species were collected from ~300 m depth with trunks up to 4.4 mm long and tails up to 10.8 mm in length. The original description (Fenaux, 1961) of the trunk and tail, the shape of the rostrum, elongated spiracles, glandular cells on the floor of the pharynx between the two spiracles, bulbous cells on the intestine, the four large cells along the bottom of the heart, paired glandular cells posteroventrally on the trunk, small digitate horns posteriorly, and the layout of the tail musculature are adequate. Nonetheless, our specimens differ in several notable respects from the original description. Fenaux based his description on 14 Mediterranean specimens of smaller size (2–3 mm trunk length) than reported here. He is very specific about only three glandular cells between the spiracles, whereas we observed six large cells and six smaller ones. He did not observe the prominent heart-shaped caudal pad on the distal third of the tail. Despite observing a large number of specimens, his illustration shows a hood that is either unique or damaged and distorted compared to our specimens. Notable differences in the gonads are likely a reflection of differences in maturity our specimens compared to his. Fenaux describes a barrel-shaped ovary, which we observe in the mature specimen where the sperm has been released and the testis is gone, while in our immature specimen the ovary is spherical. He describes the testis as simply oval, while in our immature specimen it is cylindrical. Finally, Fenaux illustrates the glandular cells on the digestive track to be bulbous while we observe them to be angular, although this is one of the few differences that might be attributed to collection and preservation differences. Although in aggregate these differences are too minor to establish a species, they do seem to be substantial enough to represent a variety. Detailed drawings are presented in the event that future collections and molecular analyses (e.g. Hebert et al., 2003) indicate that this animal is a distinct species.

DISCUSSION

Three new species and one new variety described here underscore the potential for high diversity of larvaceans in the mesopelagic realm. With only 20 *Fritillaria* specimens collected, we found four species either new to science, or unrecorded from the Pacific Ocean. More intensive sampling will undoubtedly yield more new species. In the case of both *Fritillaria rex* and *F. fagei*, body size is large compared to the remainder of species within the genus (i.e. Buckmann & Kapp,

1975). In contrast, the smallest of these species, *Fritillaria lucifer,* occurred only as by-catch during the collections of other species, rather than by targeted sampling.

In general, the anatomies of the species described in this study are consistent with those of most fritillariids (Fenaux, 1998; Bone, 1998a,b). It is notable that the morphological variation of both the trunk and the tail within the *Fritillaria* is much greater than that observed within any other larvacean genus (see e.g. Buckmann & Kapp, 1975). The three new species described have an almost tri-lobed tail distally, and the presence of distinct muscle bands that are not common in most other species. Close examination of undamaged specimens generally indicated the presence of a horn or process on the back of the trunk, with analogous structures in *Fritillaria borealis* having been implicated as a point of attachment to the food-concentrating 'house' (Flood, 2003). Only recently has the feeding structure and operation of the fritillariid house been accurately described (Flood & Deibel, 1998; Flood, 2003). The mechanism whereby the house rudiment is actually deployed is poorly described in the literature. It seems possible that the groups of cells forming the caudal pad on the anterior surface of the tail in these new fritillariid species might provide a rough and/or sticky region on the tail to help slide the house off the rostrum during deployment. (The occurrence of analogous caudal pads is undocumented in other species.) The occurrence of muscles in the pharyngeal region of *F. amphigonadis*, may also function in house deployment if they are involved in opening of the hood.

At present, we know little about the ecology of these fritillariids and their trophic roles in mesopelagic communities. Small (2 cm diameter) larvacean houses are often abundant from 150–1000 m at this study site based on quantitative video transects ongoing at MBARI for more than a decade (e.g. Robison et al., 1998, Silguero et al., 2000). A subjective estimate is that there is a relatively even mix of *Oikopleura* species (primarily *O. villafrancae*) and *Fritillaria* species, with a lesser contribution by undescribed *Mesoikopleura* species. *Fritillaria rex* was the most common of the mesopelagic fritillariids observed and collected in Monterey Bay, although this conclusion may be a reflection of its larger size rather than its true prevalence.

In general, most larvacean species have broad geographic ranges determined primarily by depth and temperature preferences (Fenaux et al., 1998), as may well be the case with several of the mesopelagic species noted at MBARI and elsewhere (Hopcroft, 2004). Two specimens that appear to be *F. rex* were collected

from the Catalina Channel in 1991–1992 (Per Flood, personal communication). It is worth noting that during most of the collection period, Monterey Bay was experiencing a strong El Niño (Chavez et al., 2002; Hopcroft et al., 2002) which may have transported more southern species northward (e.g. Lavaniegos & Ohman, 2003; Mackas et al., 2004). However, video records collected from 2000 onward have conclusively shown that *F. rex* is regularly present in Monterey Bay, as well as present outside the bay to depths in excess of 2000 m. Video records at MBARI also confirm that *F. rex* occurs at depth in the vicinity of Hawaii's Station Aloha, and in the Gulf of California. Only broader scale sampling of mesopelagic larvacean species will allow us to understand their prevalence, distribution and ecological importance.

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