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# Deep-Sea, Swimming Worms with Luminescent “Bombs”

Karen J. Osborn,<sup>1\*</sup> Steven H. D. Haddock,<sup>2</sup> Fredrik Pleijel,<sup>3</sup> Laurence P. Madin,<sup>4</sup> Greg W. Rouse<sup>1</sup>

By using remotely operated vehicles, we have collected specimens of seven species of hitherto unknown swimming annelid worms in deep waters of northeast and western Pacific Ocean (1). Specimens range in length from 18 to 93 mm and propel themselves with fans of long bristles that form swimming paddles (Fig. 1 and movie S1). Five species have four pairs of lateral, ellipsoidal organs on anterior segments that produce brilliant green bioluminescence when autotomized. All species were found between 1863-m and 3793-m depths; four live close to the seafloor (movie S2), whereas the other three are found as far as 444 m above the seafloor and are holopelagic (movie S3). Two of the demersal species were observed at densities as high as six per cubic meter. All are excellent swimmers, moving both forward and backward with use of long (at least eight-segment wave-length) metachronal waves originating posteriorly (movie S1).

These species form a previously unknown monophyletic group of acrocirrids, worms generally living in seafloor sediments. *Swima* n. gen. are swimming Acrocirridae that lack eyes and possess more than 30 long, spinous chaetae per parapodium [supporting online material (SOM) text]. The genus is typified by *Swima bombiviridis* n. sp. [holotype,

SIO-BIC (Scripps Institution of Oceanography–Benthic Invertebrate Collection) A1282, fig. S1; paratypes, SIO-BIC A1281, A1283, A1284, and A1634 to A1638], which is distinguished by its transparent foregut and greater than 15% uncorrected cytochrome oxidase I (COI) distance from all other *Swima* species. This new clade is not closely related to either of the two previously known pelagic cirratuliforms (2) and so represents a third and separate invasion of the pelagic realm within Cirratuliformia (Fig. 1E).

Green bioluminescence occurs in all the “bomb”-bearing species tested for luminosity. The luminescent structures are colloquially termed bombs because they suddenly burst into light when released by the animal, glowing intensely for many seconds then slowly diminishing. Similar autotomy of bioluminescent structures is thought to be a defensive behavior, distracting a predator while the animal escapes, and has been documented in a brittle star (3) and a squid (4). Bioluminescence for defense and reproduction is well known in many polychaetes (SOM text).

Histological study indicates the bombs are simple, fluid-filled structures with minimal internal organization, consisting of two small, central chambers and two minute, hemolymph-filled chambers on opposite poles. Both positional

homology and morphological similarities support bombs as homologous to the segmental branchiae in *Swima* species lacking bombs and other Acrocirridae (fig. S2, A to D).

The discovery of a clade of large, active, deep-sea annelids with unique morphology, bioluminescence, and high biomass emphasizes our limited knowledge of deep-sea pelagic and demersal communities.

## References and Notes

1. Materials and methods are available as supporting material on Science Online.
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3. D. Deheyn *et al.*, *J. Mar. Biol. Assoc. U. K.* **80**, 179 (2000).
4. S. L. Bush *et al.*, *Biol. Bull.* **216**, 7 (2009).
5. Research supported by Scripps Institution of Oceanography, University of California President's Postdoctoral Fellowship, David and Lucile Packard Foundation, National Oceanic and Atmospheric Administration, WHOI, and the National Geographic Society. All GenBank and voucher accession numbers are listed in table S1.

## Supporting Online Material

www.sciencemag.org/cgi/content/full/325/5943/964/DC1

Materials and Methods

SOM Text

Figs. S1 and S2

Table S1

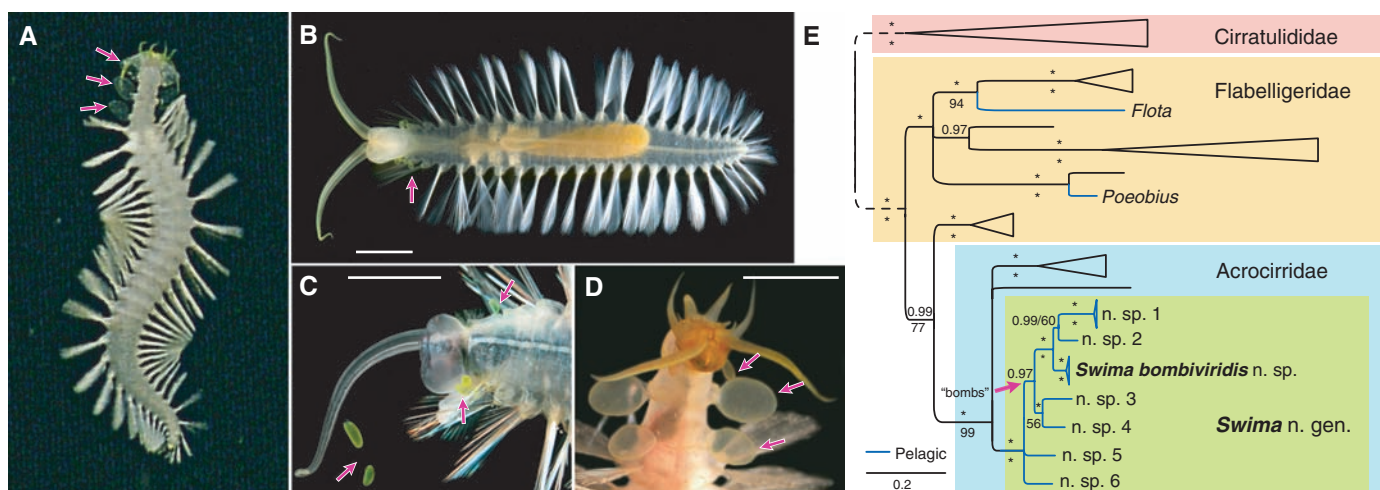
Movies S1 to S3

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**Fig. 1.** (A) Video frame grab of a *Swima* sp. 3. Arrows indicate bombs throughout. [Credit: MBARI, 2006] (B) *Swima bombiviridis* n. gen. n. sp., dorsal view; note seven bombs. Scale bars indicate 5 mm. (C) Ventral view of *Swima* sp. 1 with three attached and two autotomized bombs. [Credit: Casey Dunn, 2007] (D) Ventral view of *Swima* sp. 3 showing three pairs of attached bombs. (E) Ninety-five percent majority rule consensus tree from

Bayesian analyses of five concatenated genes from cirratuliform annelids, showing *Swima* n. gen. as part of Acrocirridae. Blue branches indicate three separate pelagic lineages. Note that Flabelligeridae is paraphyletic. Support indicated as posterior probabilities above nodes and bootstraps from a parsimony analysis below. Asterisks indicate 1.0 or 100% support, respectively (detail, fig. S2).

Supporting Online Material for:

**Deep-sea, swimming worms with luminescent “bombs”**

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This pdf file includes:

Materials and Methods

Further Results and Discussion

References

Table S1

Figure S1 and S2

Videos S1–S3 captions

## Materials and Methods

Nineteen specimens of *Swima bombiviridis* were collected by the ROV *Tiburon* outside Monterey Bay, California (2734–3497 meters, 34–36° N, 121–122° W) since the first discovery in 2001. Three specimens of *Swima* sp. 1 were collected by the ROV *Tiburon* at the above locations (3267–3625 meters). Nine specimens of *Swima* sp. 3 were collected by the ROV *Tiburon* off Santa Barbara, California (8 individuals, 1938 meters, 34° 39' 1.44" N, 121° 40' 29.64" W) and from Astoria Canyon, Oregon (1 individual, 1863 meters, 45° 55' 10.18" N, 125° 30' 8.53" W). Seven specimens of *Swima* sp. 4 and two specimens of *Swima* sp. 6 were collected with the ROV *Tiburon* off of Oregon (*Swima* sp. 4 2367 meters, 45° 30' 54.24" N, 130° 2' 26.75" W; *Swima* sp. 6 2257–2291 meters, 45° 34' 37.9–45.6" N, 130° 2' 2.85"–1' 49.11" W) in 2005. Five specimens of *Swima* sp. 5 and one specimen of sp. 2 were collected by the ROV *Max Rover Global Explorer* from the Celebes Sea, Phillipines (*Swima* sp. 5 2800–2900 meters, 4° 42–58' N, 120° 7–14' E; *Swima* sp. 2 2836 meters, 4° 58' 00" N, 120° 14' 36.6" E) in 2007. All specimens were collected using 7.5 liter detritus samplers, a high-flow suction sampler (S1), or the glass sampler (S2). Upon recovery from such depths, animals were often unresponsive and had dropped “bombs”, branchiae, and/or palps. Animals were relaxed with magnesium chloride prior to preservation in 2 % glutaraldehyde in sodium cacodylate buffer, 4–20 % formalin in seawater, 95 % chilled ethanol, or pieces in RNALater (Ambion, Austin, TX). Chaetae were imaged with differential interference contrast and with a scanning

electron microscope. Dissected branchiae, papillae, and bombs were embedded in Spurr's resin, sectioned, and stained with toluidine blue. The anterior portion of a *S. bombiviridis* and a *Swima* sp. 3 were embedded in wax, sectioned, and stained with 0.1 % aqueous *azureA*.

In order to resolve relationships of the new species to known Cirratuliformia, all non-redundant and reliable flabelligerid, acrocirrid, and cirratulid sequences, for which at least two of the five study genes were available, were included in this project (Table S1). Of the Cirratuliformia, the new species were most morphologically similar to acrocirrids and flabelligerids and least similar to cirratulids. Cirratulids were chosen as the root based on morphological (*S3, S4, S5*) and molecular attempts to resolve relationships within Annelida (*S6, S7, S8*). Cirratulids rooted the tree such that flabelligerids were paraphyletic and contained a monophyletic Acrocirridae. This requires reversals of complex morphological characters in the relatively simple-bodied acrocirrids with respect to flabelligerids and further investigation into the relationship between these two taxa is warranted. It should also be noted that Cirratulidae form a long branch with respect to Flabelligeridae and Acrocirridae, suggesting the root location requires further assessment. These issues are beyond the scope of this investigation and do not impact the monophyly or naming of the new clade. DNA sequence methods were described in detail in (2) with the addition of the sequences indicated in bold (Table S1) and the use of Qiagen DNeasy tissue kit (Valencia, CA) for all new extractions.

Sequences were concatenated only when from the same extraction except in six cases for which extracts were not available (Table S1 shaded pairs). Sequences were aligned with MUSCLE 3.6 (S9) using default settings and proofread by eye in MacClade v.4.04 OS X (S10). Neither ambiguously aligned bases nor third codon positions were removed from analyses (individual alignments: *18S*, 2083 base pairs, *28S*, 1329 base pairs, *COI*, 681 base pairs, *CytB*, 390 base pairs, *16S*, 546 base pairs). The complete alignment is available from KJO or at TreeBase.

Bayesian analyses of the data sets were conducted using MrBayes 3.1.2 (S11). Standard procedures based on Modeltest 3.5 (S12) were implemented in PAUP\* 4.0b10 to select the most appropriate models for individual genes. The relative fit of models was assessed by the Akaike information criterion. Smaller values of *AIC* are preferred (S13, S14) and the General Time Reversible + Proportion Invariant + Gamma (GTR+I+ $\Gamma$ ) represented the optimal model with respect to all genes. Partitions were unlinked in the concatenated analyses. Each Markov chain, three heated and one cold, was started from a random tree and all four chains were run simultaneously for 5 to 50 million generations, with trees being sampled such that the resulting data set from each run contained at least 10,000 data points after burn-in. AWTY (S15) was used to determine if a sufficient number of generations had been completed for posterior probabilities to stabilize, as well as to determine amount of required burn-in before inference from the MCMC data set was made. Repeated analyses converged on similar

parameter estimates.

Parsimony analyses were conducted with PAUP\* 4.0b10 (*S16*) using an equally weighted character matrix, the heuristic search option, the tree-bisection-reconnection branch-swapping algorithm, and 1000 random addition replicates. Gaps were treated as missing data. Bootstrap values were obtained with the same settings as the parsimony analysis (1000 replicates). There were 1743 parsimony informative characters from the complete 5029 base-pair alignment.

## **Further Results and Discussion**

### *Bioluminescence*

Specimens were recovered in various conditions, from alive and undamaged to severely damaged and dead. Despite this range, zero to eight bombs were found attached to recovered specimens with no correlation between the degree of damage and the number of bombs remaining. Live specimens were recovered with up to eight bombs, a full complement. These bombs were observed in various states of regeneration (judged by size) within single individuals. The ROV's lights and camera capabilities coupled with the size of the bombs (typically less than one mm) did not allow observation of bomb release *in situ*. Once recovered, manual stimulation of the animal at any point along the body or head would result in the release of a bomb or two, which would immediately bioluminesce. Further stimulation would result in release of additional bombs if they were available. It is assumed based on 1) laboratory observations, 2) the

various states of bomb regeneration within single individuals, and 3) the number of bombs still attached to recovered specimens that they are not all released at one time *in situ* and that disturbance caused by observation and collection with the ROV is not significant enough to cause release of all bombs. It is unfortunate that since bomb release *in situ* is not observable, we cannot at this time determine potential predators reaction to the release of bombs.

Bioluminescence is a known defensive tool in polychaetes. When severed, the posterior end of *Eusyllis bromstrandii* (Syllidae) continues to glow for several seconds while the light in the anterior region is immediately extinguished (S17, S18). *Odontosyllis* species (Syllidae) produce bioluminescence as a startle response (S19), as do *Chaetopterus* (S20). Many scaleworms (Aphroditoidea) are known to slough manually stimulated scales that continue to glow (S21). We suggest that the use of bioluminescent bombs seen in some *Swima* species is not associated with reproduction, but instead serves a defensive function. The nature of the bioluminescent structures, observation of autotomization of these structures in response to stimulation at multiple points along the body, luminescence of the structures after release, and the presence of bioluminescence in immature and mature specimens supports this hypothesis.

### *Systematics*

*Swima*, complementary description

Type species, *Swima bombiviridis*, by original designation



### *Etymology*

Named for members' ability to swim. The name is treated as an arbitrary combination of letters and is designated as feminine by the addition of the Latin singular, first declension, nominative ending *-a*.

### *Diagnosis*

Swimming acrocirrids with more than 30 long (more than body width) chaetae per parapodium. Eyes absent. Head not retractable. With thick or thin gelatinous sheath penetrated by clavate papillae. One or more lollipop-shaped, interramal papillae projecting well beyond gelatinous sheath. Nuchal organs just posterior to palps as simple oblique, slightly raised ridges to spiral and branched structures free-standing above body wall. Four pairs of branchiae that may be modified as ellipsoid bioluminescent structures or elongate (more than half body length) with tapered distal tips. Branchiae easily lost, leaving obvious circular scars.

### *Remarks*

*Swima* n. gen. shares the following features with other Acrocirridae: achaetous anterior segments (Figs. S2A–D), shape of prostomium (Figs. S2B–C), nephridopore near second branchiae, gonads in three or less anterior segments, four or less easily lost branchiae (Figs. S2A–D), and simple, spinous notochaetae. *Swima* differs from *Macrochaeta* Grube, 1850, *Acrocirrus* Grube,

1872, *Flabelligella* Hartman, 1965, and *Flabelligena* Gillet, 2001 in general body form, the absence of eyes, and presence of more than 30 chaetae per parapodium (Figs. 1, S1, S2). *Swima* differs from *Flabelliseta incrusta* Hartman, 1978 in the shape of the notopodial papillae, possessing notochaetae, and by not adhering sediment particles to their gelatinous sheath. *Swima* is most similar to *Helmetophorus rankini* Hartman, 1978 and *Chauvinelia* (consisting of *C. biscayensis* Laubier, 1974 and *C. arctica* Averintsev, 1980). These three genera share the nature of their buccal organ and possibly the ability to swim, although the latter is unconfirmed in *Chauvinelia* and *Helmetophorus*. *Swima* differs from *Helmetophorus* and *Chauvinelia* by lacking a retractable head. *Swima* and *Chauvinelia* further differ from *Helmetophorus* by possessing lollipop-shaped interramal papillae, much larger body size, and more than 30 chaetae per parapodium.

*Swima* n. gen. forms a well-supported clade distinct from all previously known acrocirrids and flabelligerids available for these analyses (Fig. S2). *Helmetophorus*, *Chauvinelia*, *Flabelliseta*, and *Flabelligella* were unavailable for genetic analyses, but as detailed above, they are distinguishable from *Swima* based on morphology. *Helmetophorus* and *Chauvinelia* are the most likely candidates to form a clade with *Swima*, but their retractable heads ally them to flabelligerids and possibly *Flabelligella* (S22), serving as a complex character that clearly distinguishes these two genera from *Swima*.

*Swima bombiviridis*, complementary description

Figures 1B and S1

*Type material*

Holotype, collected off the central coast of California 7 April, 2005 at 3054 meters in 3498 meter deep water by KJO and SHDH, deposited at the Benthic Invertebrate Collection of Scripps Institution of Oceanography (SIO BIC A1282; 36° 19.80' N, 122° 53.99' W). Eight paratypes collected by KJO (SIO BIC A1281 and A1284 5 June 2005 3744 meters, 36° 43.98' N, 123° 41.93' W; SIO BIC A1283 28 November 2007 3019 meters, 35° 50.42' N, 122° 40.13' W; SIO BIC A1634–1635 20–21 September 2005 3325–3442 meters, 36° 19.80' N, 122° 53.99' W; SIO BIC A1636 2 October 2006 2732 meters, 35° 37.99' N, 122° 44.00' W; SIO BIC A1637 2 November 2007 3411 meters, 36° 19.39' N, 122° 54.18' W; SIO BIC A1638 26 February 2009 3600 meters, 35° 7.61' N, 122° 55.60' W) are deposited at the Scripps Institution of Oceanography Benthic Invertebrate Collection.

*Etymology*

Named for the common name used for the group, green bombers. *Bombus* is the Latin root meaning humming or buzzing from which the English word bomb is derived. *Viridis* is Latin for green.

### *Diagnosis*

*Swima* with transparent gut. Possessing a thick, transparent gelatinous sheath penetrated throughout by narrow clavate papillae, simple noto- and neurochaetae, and three achaetous anterior segments supporting ellipsoid, bioluminescent, derived branchiae that are less than 1.5 mm in length.

### *Holotype description*

*Body* transparent, 25 chaetigers with distinct parapodial lobes and numerous long chaetae, posterior half smoothly tapered with thick gelatinous sheath through which narrow, clavate papillae extend (Fig. 1B). Total body length, when alive, over 15 mm. Small, clavate papillae clear or yellow in life, extend from body wall through gelatinous sheath, especially numerous on parapodia and dorsum of anterior segments. One to four large, white to brown, lollipop-shaped papillae interrampal on each parapodium, largest found on second chaetiger (Figs. S1A–D). Pygidium unadorned (Fig. S1D).

*Head* consists of prostomium, peristomium, and at least two achaetous segments possessing three forms of branchiae (Figs. S1A–C; but see *Variation*). Prostomium consists of tissue posterior to palp attachments, supporting pair of low, ciliated, oblique ridges that form nuchal organs. No eyes. Grooved frontal palps transparent to yellow in life, tapered, coiling at tips, long, reaching at least fourth chaetiger (Fig. S1C). Peristomium surrounds prostomium completely. Buccal organ antero-ventrally located, unarmed, bilobed, forming eversible lateral

lips (Fig. S1A). Lateral lips and inner lobe lacking pigment. Three forms of branchiae: 1) single, long (reaching at least second chaetiger), tapered/subulate median branchia, transparent to white (Figs. S1A and C), 2) more than 40, fine, digitiform respiratory branchiae present across lateral and dorsal surface in tightly packed row, yellow in life (Figs. S1A–C), and 3) four elliptical lobes attached to achaetous anterior segments posterior to median and digitiform branchiae and one on first chaetiger. Segmentally-occurring, elliptical, lobe-like branchiae greenish-yellow in life, autofluoresce the same color, produce bioluminescence, often autotomized. Bombs 0.7 to 1.1 mm in length. Scars from bombs distinguishable as slightly raised rings of thickened tissue, colloquially referred to as “bomb bays” (Fig. S1B). Four pairs bomb bays: one slightly ventral from lateral midline just posterior to the digitiform branchiae, one posteriorly located on medial half of nephridiopore, one posterior to nephridiopore at lateral midline, and one posterior to chaetae on first notopodium. Slight ridge posterior to nuchal organs and anterior to median and digitiform branchiae, possibly indicating segment margin.

*Chaetigers* similar along body. Noto- and neuropodal lobes form single, nearly smooth projection with higher concentration of fine clavate papillae compared to rest of body surface (Fig. S1E). One to four clavate papillae having rounded bulbous tips and narrow bases ("lollipop" shaped) found between noto and neuropodial lobes, project well beyond gelatinous sheath (Figs. S1A–D), tips are solid, not hollow like those found in *Flabelliseta*. Noto and neurochaetae

indistinguishable except by position, simple, with no articulations (Fig. S1G). High magnification reveals fine whorls of spines along entire length chaetae giving especially distal tips segmented appearance, bases appearing striated under high magnification (Figs. S1F–H). Distal edge of spinous whorls project as frayed edges on worn and longest chaetae. Chaetigers 4–6 each with a pair of low, hollow papillae (gonopore) at ventral base of neuropodia (Fig. S1A).

*Internal anatomy* visible through transparent body wall and gelatinous sheath. Ventrally located double nerve cord with two pairs fused ganglia per segment, diverges just posterior to peristomium to surround buccal organ, fuses again just posterior to palp attachment. Single pair of large anterior, semitransparent nephridia reaching back as far as second chaetiger, ventrally oriented from lateral origin, overlapping each other in ventral portions first and second chaetiger, folding back antero-dorsally, then narrowing to lead to lateral nephridiopores. Gut running from buccal organ straight for one third body length (approximately to chaetiger 8) at which point it forms wide, single loop, after which it broadens and continues back to approximately twelfth chaetiger before narrowing and turning anteriorly again. Gut continues anterior to near first loop then folds rearward and continues directly to pygidium (Fig. S1C). Heart body first distinguishable just posterior to digitiform branchiae, extends through the anterior one third of body until it appears to fuse with anterior-most dorsum of broadened portion of gut. Gonads form at posterior margin of chaetigers 4–6 (Fig. S1A).

### *Variation*

Specimens with 21–30 chaetigers, reaching at least 32 mm body length. Palps easily lost, leaving obvious scars, sometimes varying in length relative to body length. Bombs easily lost, even during gentle collection, found on the floor of the sampling device upon recovery of the ROV or dropped in dishes during laboratory examination. More than one bomb was never observed attached to a single bomb bay. Various sized bombs found on single individuals ranging from 0.6–1.2 mm. Most anterior pair bombs often smaller than following pairs. Smaller bombs spherical while larger bombs elliptical. Length of single, median branchia varied relative to body length, seldom lost, with obvious scar when lost. Digitiform branchiae not easily lost, but absent from five of the eight specimens confirmed as belonging to this species via DNA sequences.

Preserved specimens sometimes appear to have a slightly eversible head because contraction and shrinking during preservation shortens individual anterior segments sinking them slightly into the gelatinous sheath. This was never seen in live specimens, even when manually stimulated, or those fully relaxed before preservation. Further, there is no fold of the body into which the head can be drawn nor large muscles, as seen in flabelligerids, that enable evagination of the anterior end. When the anterior segments are contracted, it can be difficult to see the bomb bays and segment margins but attached bombs and the single median branchia are always visible.

### Remarks

This species is most similar to *Swima* sp. 1 (Fig. 1C) and *Swima* sp. 2. The transparent gut and unpigmented buccal organ together with the genetic differences found in *COI* and *CytB* sequences (15 % and 12–13 % uncorrected distances respectively) separate the three species. Additionally, specimens of *Swima* sp. 1 tend to be larger and have more tapered anterior and posterior ends than those of *S. bombiviridis*. *Swima* sp. 2 differs from *S. bombiviridis* and *Swima* sp. 1 in the extreme flatness of their chaetae, possessing pseudocompound neurochaetae, possessing a pair of lateral subulate branchiae, and a 180-degree curve at the dorso-medial end of the nuchal ridge. *Swima bombiviridis* differs from *Swima* sp. 3 (Figs. 1A and E) and *Swima* sp. 4 by relative size of bombs, lacking pseudocompound neurochaetae, simplicity of nuchal ridge, lacking numerous subulate branchiae, thickness of gelatinous sheath, transparency of body, and position of gonopores. *Swima bombiviridis* differs from *Swima* sp. 5 (Fig. S2A) and *Swima* sp. 6 (Fig. S2C) by possession of bombs instead of elongate branchiae, degree of flattening of chaetae, lacking pseudocompound neurochaetae, possession of simple nuchal ridges instead of free-standing nuchal structures, number of achaetous segments, location of gonopores, and thickness of gelatinous sheath. All species were genetically distinct from each other (15–22 % uncorrected *COI* distances, 12–22 % *CytB*, 0.06–0.9 % *18S*, 0.5–3 % *28S*, 5–39 % *16S*).



## *Ecology*

*Swima bombiviridis* is found off the central California coast at 2732–3600 meters depth, from 1–444 meters above the seafloor. Similar animals were observed but not collected (species identification is unconfirmed) off the Oregon coast (45°24.02' N, 126° 43.00' W), as well as the Gulf of California (24° 18.99' N, 109° 11.95' W). Animals were not observed on the seafloor although they were sometimes observed within sight of it.

Animals were most often observed hanging horizontally in the water column with the palps hanging forward and downward over the buccal organ, which typically projects antero-ventrally. The species, like others in the clade, swim by lateral undulation of the body coupled with expansion on the power stroke and contraction on the recovery stroke of the chaetal fans. Swimming was observed in both forward and rearward directions, which were difficult to distinguish unless the ROV was completely still and camera zoomed in enough to identify the anterior end. Animals were seldom observed *in situ* in close enough detail to determine the direction of their initial swimming when disturbed, but in the three instances where it was possible, direction of initial escape was always rearward. This is consistent with the direction of escape swimming observed in other *Swima* species.

Bioluminescence was seen as a steady glow from bombs that had been autotomized from the body of the animal. Bombs that were separated from the

animal could again be triggered to produce light by gently squeezing them with forceps. The glow of an individual bomb lasted several seconds.

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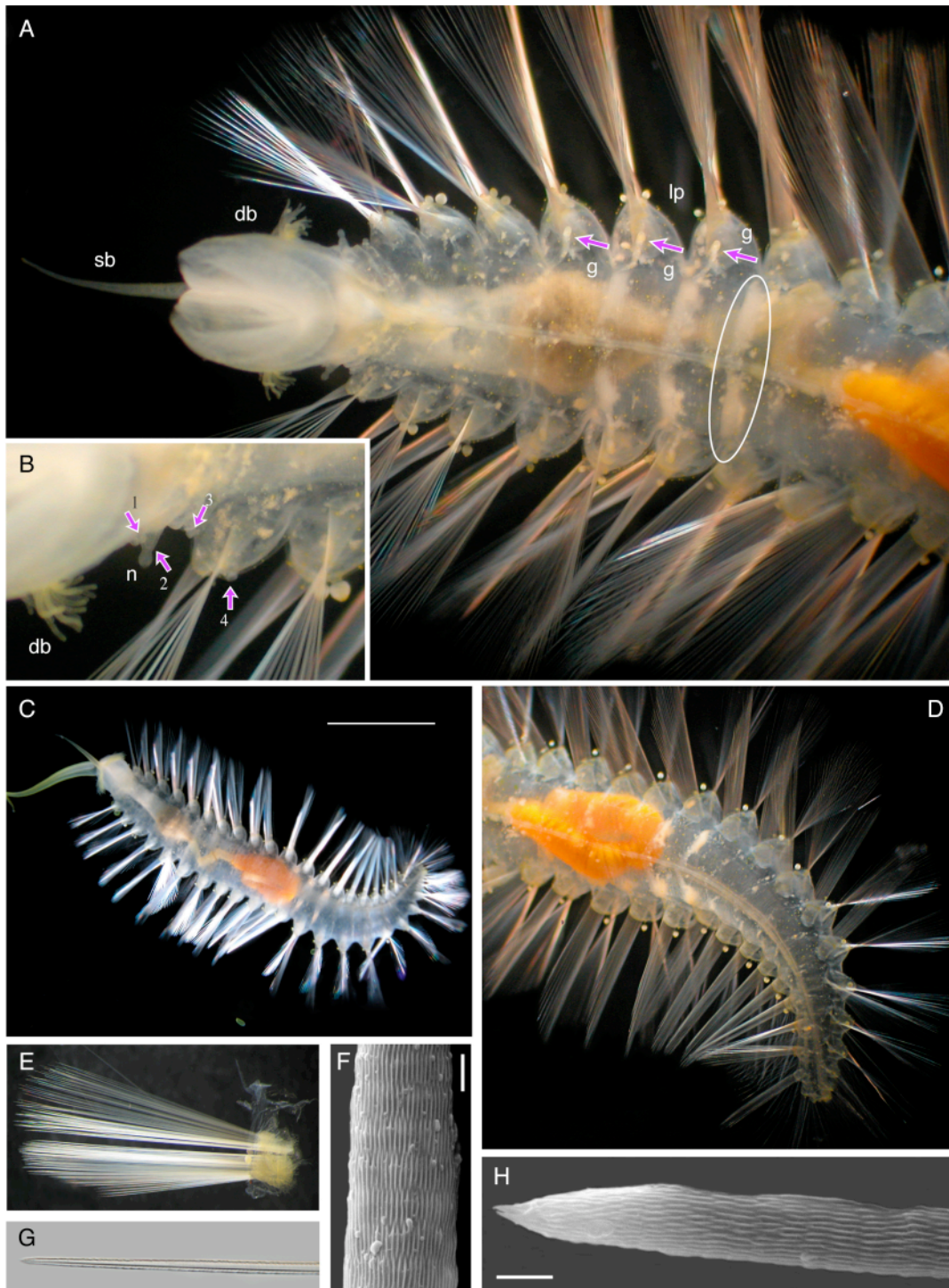
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**Table S1.** GenBank and voucher accession numbers. Shaded pairs were concatenated. GenBank numbers in bold indicate new sequences. Superscripts indicate citation for previously published sequences.

Taxon	18S	28S	COI	CytB	16S	Voucher	Locality
<b>Acrocirridae</b>							
<i>Acrocirrus validus</i> Marenzeller, 1879	<b>FJ944491</b>	-	<b>FJ944525</b>	<b>FJ944538</b>	-	SIO BIC A1290	Hayama, Sagami Bay, Japan
<i>Flabelligena</i> sp.	EU694120	EU694121	EU694126	EU694135	EU694113	SIO BIC A1126	Pacific Antarctic Ridge <sup>2</sup>
<i>Macrochaeta clavicornis</i> (Sars, 1835)	EU791461	-	EU791463	-	-	SIO BIC A1087	Vattenholmen, Sweden <sup>2</sup>
<i>Macrochaeta clavicornis</i> (Sars, 1835)	-	DQ779696	-	-	-	SMNH 75829	Bohuslän, Sweden <sup>2</sup>
<i>Macrochaeta</i> sp.	EU700414		EU694125	EU694136	EU694114	SIO BIC A1127	Belize <sup>2</sup>
<i>Swima bombiviridis</i> (PB44, hologenophore)	<b>FJ944493</b>	<b>FJ944516</b>	<b>FJ944526</b>	<b>FJ944539</b>	<b>FJ944505</b>	SIO BIC A1281	Monterey, California
<i>Swima bombiviridis</i> (PB51, hologenophore)	-	-	<b>FJ944527</b>	<b>FJ944540</b>	<b>FJ944506</b>	SIO BIC A1282	Monterey, California
<i>Swima bombiviridis</i> (P9, hologenophore)	<b>FJ944494</b>	<b>FJ944517</b>	<b>FJ944528</b>	<b>FJ944541</b>	<b>FJ944507</b>	SIO BIC A1283	Monterey, California
<i>Swima bombiviridis</i> (PB39, hologenophore)	<b>FJ944495</b>	-	<b>FJ944529</b>	<b>FJ944542</b>	<b>FJ944508</b>	-	Monterey, California
<i>Swima bombiviridis</i> (PB42, hologenophore)	<b>FJ944496</b>	<b>FJ944518</b>	<b>FJ944530</b>	<b>FJ944543</b>	<b>FJ944509</b>	SIO BIC A1284	Monterey, California
<i>Swima</i> sp. 1 (ind. PB32)	<b>FJ944497</b>	-	<b>FJ944531</b>	<b>FJ944544</b>	-	SIO BIC A1285	Monterey, California
<i>Swima</i> sp. 1 (ind. P1)	<b>FJ944498</b>	<b>FJ944519</b>	<b>FJ944532</b>	<b>FJ944545</b>	<b>FJ944510</b>	SIO BIC A1286	Monterey, California
<i>Swima</i> sp. 2	<b>FJ944499</b>	<b>FJ944520</b>	<b>FJ944533</b>	<b>FJ944546</b>	<b>FJ944511</b>	Nat. Mus. Philippines NMA 0437	Celebes Sea, Philippines
<i>Swima</i> sp. 3	<b>FJ944500</b>	<b>FJ944521</b>	<b>FJ944534</b>	<b>FJ944547</b>	<b>FJ944512</b>	SIO BIC A1287	Astoria Canyon, Oregon
<i>Swima</i> sp. 4	<b>FJ944501</b>	<b>FJ944522</b>	<b>FJ944535</b>	<b>FJ944548</b>	<b>FJ944513</b>	SIO BIC A1288	Juan de Fuca Ridge, Oregon

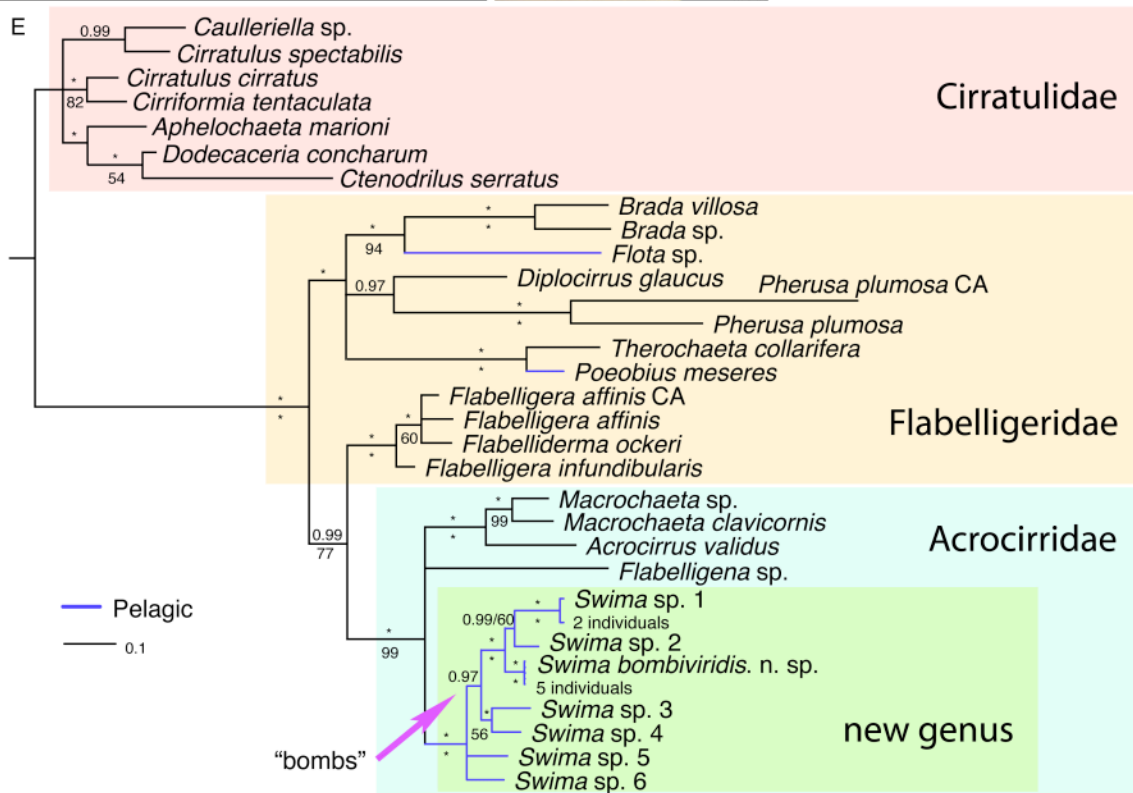
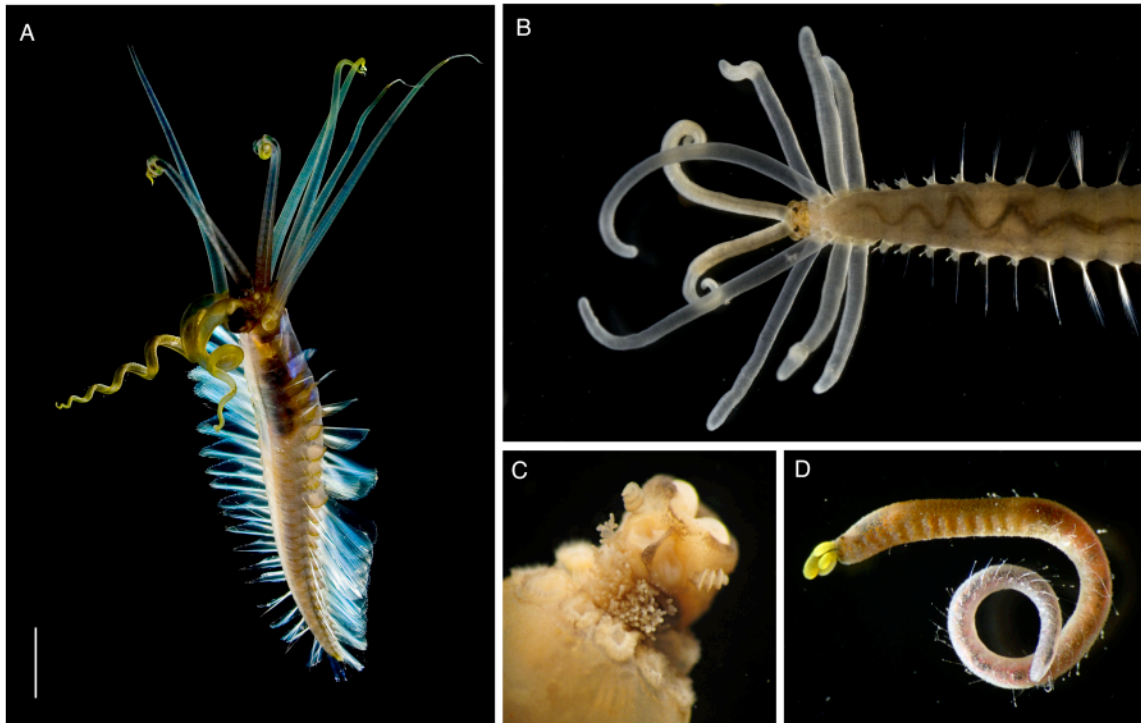
Taxon	18S	28S	COI	CytB	16S	Voucher	Locality
<i>Swima</i> sp. 5	FJ944503	FJ944524	FJ944537	FJ944550	FJ944515	Nat. Mus. Philippines pending	Celebes Sea, Philippines
<i>Swima</i> sp. 6	FJ944502	FJ944523	FJ944536	FJ944549	FJ944514	SIO BIC A1289	Juan de Fuca Ridge & Axial Seamount, Oregon
<b><i>Flabelligeridae</i></b>							
<i>Brada villosa</i> (Rathke, 1843)	EU791460	EU791462	-	-	-	SIO BIC A1161	Fiskebäckskil, Sweden <sup>2</sup>
<i>Brada villosa</i> (Rathke, 1843)	-	-	-	AY727747	-	USNM 1073357	Trondheimsfjord, Norway <sup>S6</sup>
<i>Diplocirrus glaucus</i> (Malmgren, 1867)	AY708534	DQ790031	-	AY727751	-	USNM 1073353	Gullmarsfjorden, Sweden <sup>S6, S8</sup>
<i>Diplocirrus glaucus</i> (Malmgren, 1867)					FJ944504	SIO BIC A1139	Kristineberg, Sweden
<i>Flabelliderma ockeri</i> Salazar-Vallejo, 2007	EU694119	-	EU694127	EU694137	EU694111	SIO BIC A1129	La Jolla, California, USA <sup>2</sup>
<i>Flabelligera affinis</i> Sars, 1829	AY708532	-	-	-	-	USNM 1073354	Gullmarsfjorden, Sweden <sup>S6</sup>
<i>Flabelligera affinis</i> Sars, 1829	-	DQ779688	-	-	DQ779614	SAM E3562	Iceland <sup>S7</sup>
<i>Flabelligera affinis</i> Sars, 1829	AY708531	-	-	AY727755	-	USNM 1073355	Central California, USA <sup>S6</sup>
<i>Flabelligera infundibularis</i> (Johnson, 1901)	EU694118	EU694124	EU694131	EU694133	EU694112	SIO BIC A1128	Astoria, Oregon, USA <sup>2</sup>
<i>Flota</i> sp.	EU694116	EU694110	EU694128	EU694134	EU694110	SIO BIC A1131	Monterey, California, USA <sup>2</sup>
<i>Pherusa plumosa</i> (Müller, 1776)	AY708529	-	-	AY727756	-	USNM 1073348	Woods Hole, Massachusetts, USA <sup>S6</sup>
<i>Pherusa plumosa</i> (Müller, 1776)	AY708528	DQ790056	-	AY727752	-	USNM 1073356	Central California, USA <sup>S6, S8</sup>
<i>Poeobius meseres</i> Heath, 1930	EU694115	EU694123	EU694130	EU700415	-	SIO BIC A1130	Monterey, California, USA <sup>2</sup>
<i>Poeobius meseres</i> Heath, 1930	-	-	-	-	DQ779631	SAM E3563	Monterey, California, USA <sup>2</sup>
<i>Therochaeta collarifera</i> Ehlers, 1887	AY708527	-	-	AY727753	-	USNM 1073350	Woods Hole, Massachusetts, USA <sup>S6</sup>

Taxon	18S	28S	COI	CytB	16S	Voucher	Locality
<b><i>Cirratulidae</i></b>							
<i>Aphelochaeta marioni</i> (Saint Joseph, 1894)	DQ779639	DQ779674	-	-	DQ779602	SAM E3559	Iceland <sup>S7</sup>
<i>Dodecaceria concharum</i> Örsted, 1843	AY577891	DQ209242	DQ209262	-	-	SAM E3355	Iceland <sup>S23</sup>
<i>Dodecaceria concharum</i> Örsted, 1843	-	-	-	-	<b>FJ965555</b>	SIO BIC A1141	Bohuslän, Sweden
<i>Caulleriella</i> sp.	-	DQ779679	-	-	DQ779606	SAM E3560	Iceland <sup>S7</sup>
<i>Cirratulus cirratus</i> (Müller, 1776)	DQ779645	DQ779683	-	-	DQ779609	SAM E3561	Iceland <sup>S7</sup>
<i>Cirratulus spectabilis</i> (Kinberg, 1866)	AY708536	DQ790029	-	AY727746	-	USNM 1073359	Snug Harbor, Washington, USA <sup>S8</sup>
<i>Cirriformia tentaculata</i> (Montagu, 1808)	AY611456	AY611443	-	-	-	-	Banyuls, France <sup>S24</sup>
<i>Ctenodrilus serratus</i> (Schmidt, 1857)	AY340426	AY340388	-	-	AY340452	-	Massachusetts, USA <sup>S7</sup>



**Fig. S1.** Holotype *Swima bombiviridis* n. gen. n. sp., A–D from live specimen. **(A)** Ventral view of anterior. Median subulate branchia (sb), digitiform branchiae (db), lollipop-shaped papillae (lp), and gonopores (g, arrows) are indicated as are the posterior-most developing gonads at the margin of chaetigers 6 and 7 (white oval). **(B)** Close up of scars left from autotomized “bombs” (“bomb bays”) seen as small rings of raised tissue and labeled 1–4 from anterior to posterior, digitiform branchiae, and the nephridiopore (n) on which bomb bay 2 is found. **(C)** Dorsal view of whole animal showing one detached bomb at the bottom of the image, numerous short digitiform branchiae, the median subulate branchia, and a single remaining grooved palp. **(D)** Ventral view of posterior end showing interramal lollipop papillae and posterior gut loops. **(E)** Parapodium showing notochaetae above and neurochaetae below, two interramal lollipop papillae, and fragments of gelatinous sheath. **(F)** Scanning electron micrograph of shaft of a chaeta. **(G)** Differential interference light micrograph of distal tip of a chaeta. **(H)** Scanning electron micrograph of distal tip of a chaeta. Scale bars C = 5 mm, F and H = 2  $\mu\text{m}$ .





**Fig. S2. (A)** Left ventro-lateral view of *Swima* sp. 5 showing seven elongate branchiae, coiled, grooved palps, and chaetal fans. Scale bar, 10 mm. **(B)** *Acrocirrus validus* Marenzeller, 1879 in dorsal view showing the four pairs of elongate branchiae just posterior to the head, grooved palps, and eyes. **(C)** Dorsal view of head of *Swima* sp. 6 showing spiral and branched, free-standing nuchal structures, palp scars, and elongate branchiae scars. **(D)** *Flabelligena* sp. in lateral view showing three short branchiae and one grooved palp. **(E)** Ninety-five percent majority rule consensus tree from Bayesian analyses of five concatenated genes from cirratuliform annelids, showing *Swima* n. gen. as part of Acrocirridae. Blue branches indicate three separate pelagic lineages. Note Flabelligeridae is paraphyletic when rooted with Cirratulidae. Support indicated as posterior probabilities above nodes, bootstraps from the parsimony analysis below. Asterisks indicate 1.0 or 100 % support respectively.

**Video S1.** *Swima* sp. 3 swimming *in situ*, Astoria Canyon, Oregon, 1863 meters depth.

**Video S2.** Numerous *Swima* sp. 3 swimming just off, landing on, and taking off from the seafloor, off Santa Barbara, California, 1938 meters depth.

**Video S3.** Unusual sighting of five *Swima bombiviridis* n. gen. n. sp. swimming in a group, Astoria Canyon, Oregon, 2243 meters depth. Possibly a mating swarm.