

The remarkable squidworm is an example of discoveries that await in deep-pelagic habitats

Karen J. Osborn, Laurence P. Madin and Greg W. Rouse

Biol. Lett. published online 24 November 2010
doi: 10.1098/rsbl.2010.0923

Supplementary data

"Data Supplement"

<http://rsbl.royalsocietypublishing.org/content/suppl/2010/11/19/rsbl.2010.0923.DC1.html>

References

This article cites 12 articles, 1 of which can be accessed free

<http://rsbl.royalsocietypublishing.org/content/early/2010/11/19/rsbl.2010.0923.full.html#ref-list-1>

P<P

Published online 24 November 2010 in advance of the print journal.

Subject collections

Articles on similar topics can be found in the following collections

[taxonomy and systematics](#) (299 articles)
[evolution](#) (2221 articles)

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

Advance online articles have been peer reviewed and accepted for publication but have not yet appeared in the paper journal (edited, typeset versions may be posted when available prior to final publication). Advance online articles are citable and establish publication priority; they are indexed by PubMed from initial publication. Citations to Advance online articles must include the digital object identifier (DOIs) and date of initial publication.

To subscribe to *Biol. Lett.* go to: <http://rsbl.royalsocietypublishing.org/subscriptions>

The remarkable squidworm is an example of discoveries that await in deep-pelagic habitats

Karen J. Osborn^{1,*}, Laurence P. Madin² and Greg W. Rouse¹

¹*Scripps Institution of Oceanography, 9500 Gilman Drive, La Jolla, CA 92093-0202, USA*

²*Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA*

**Author for correspondence (kosborn@ucsc.edu).*

[†]*Present address: University of California, Santa Cruz, Institute of Marine Sciences, 1156 High Street, Santa Cruz, CA 95064, USA*

An intriguing new annelid, *Teuthidodrilus samae* (Annelida, Cirratuliformia) gen. and sp. nov., was observed and collected during deep-water column exploration of the western Celebes Sea. The Celebes Sea is a deep pocket basin, effectively isolated from surrounding deep water, and is part of the Coral Triangle, a focal area for conservation because of its high diversity and unique geological history. Collected specimens reached 94 mm in length and possessed 10 anterior appendages that were as long or longer than the body. Two characters distinguish *T. samae* from other polychaetes: notochaetae forming broad, concavo-convex paddles and six pairs of free-standing, oppositely branched nuchal organs. Phylogenetic analysis of five genes and a 29-character morphological matrix showed that *T. samae* is an acrocirrid (primarily benthic polychaetes) belonging to the morphologically diverse swimming clade. Pelagic animals within primarily benthic clades are of particular interest in evolutionary biology, because their adaptations to life in the water column inform us of the evolutionary possibilities and constraints within the clade and indirectly of the selective pressures at work in this unfamiliar habitat. This new genus illustrates how much we have to learn about even the large, abundant inhabitants of deep-pelagic communities.

Keywords: Acrocirridae; Celebes Sea; pelagic; Polychaeta; *Teuthidodrilus samae*

1. INTRODUCTION

The Celebes Sea (figure 1a) is a deep basin (maximum depth approx. 6200 m) located between the Philippines and Indonesia, which is thought to have formed in the Eocene (44–42 Myr ago) far from any major land mass [1]. During the Pleistocene, the basin was isolated by significantly lower sea level that exposed surrounding islands. The deep-water habitat of the Celebes basin continues to be isolated from surrounding deep water by relatively shallow sills (approx. 500 m to a maximum depth of 1350 m). Density differences inhibit water flowing over the sills from

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2010.0923> or via <http://rsbl.royalsocietypublishing.org>.

Received 4 October 2010
Accepted 4 November 2010

mixing with basin water, resulting in long residence times for water below 1500 m [2]. The basin is at the centre of the Coral Triangle, an area now considered a conservation hotspot owing to the high diversity and endemism of shallow-water corals and fishes [3]. This area is also the centre of geographical distributions and diversity of lanternfish, hatchetfish, dragonfish and anglerfish [4]. Based on the unique geology and history of the basin and the extreme diversity of the shallow-water fauna, the hypothesis that the deep fauna may be equivalently diverse and unique was a motivation for the exploratory expedition to the Celebes Sea.

Animal density typically decreases with depth in the open ocean but then increases again when approaching the deep-sea floor [5–7]. The concentration of mobile animals within a few hundred metres of the seafloor forms a diverse demersal community that we know little about. Many organisms found in this broad demersal or benthic-pelagic zone (the bottom several hundred metres that is influenced by the seafloor) have long been inaccessible for two main reasons. First, traditional sampling gear was designed to collect benthic (living on the seafloor) or pelagic (living in the water column) animals. Swimming organisms can escape collection devices towed on the seafloor and midwater nets are not often towed near the seafloor at great depth because of the risk of damaging the relatively fragile gear [8]. Second, many of the community's animals are delicate and thus damaged beyond usefulness by indiscriminate sampling gear and the long trip back to the surface [9]. Development of vehicles capable of free operation in the deep-water column has allowed direct access to deep-pelagic habitats. These vehicles have the unique ability to observe animals undisturbed in their natural habitat and to collect them without damage, and thus are providing a more complete picture of the inhabitants of the largest habitat on the Earth [10–11].

Here, we introduce *Teuthidodrilus samae* (figure 1b), an unusual new genus and species of swimming polychaete from the deep benthic-pelagic zone of the Celebes Sea discovered by direct observation with a remotely operated vehicle. We also present notes on this species' behaviour and ecology in the electronic supplementary material. Based on combined molecular and morphological analyses, *T. samae* gen. and sp. nov. belongs to Acrocirridae, is a member of the swimming clade (figure 1c) and is sister to the 'bomb'-bearing clade [12]. *Teuthidodrilus samae* gen. and sp. nov. is an example of the type of discoveries we can anticipate with continued exploration of the least known and largest habitat on the Earth, the deep-water column.

2. MATERIAL AND METHODS

Seven specimens of *T. samae* were collected from the deep-water column of the Celebes Sea in October of 2007 (table 1). All *in situ* observations were made with the remotely operated vehicle *Max Rover Global Explorer* operated from Philippines research vessel BRP *Hydrographer Presbitero*. *In situ* video was taken with a Panasonic high-definition camera. Specimens were captured in 6.5 l detritus samplers or with a high-flow suction sampler [13]. Live specimens were photographed immediately, then relaxed in magnesium chloride and fixed in formalin. Tissue removed from three animals was placed in chilled 95 per cent ethanol for genetic analysis.

Specimens were examined in the laboratory with light and scanning electron microscopy. Dissected branchiae and chaetae were embedded in Spurr's resin, sectioned and stained with toluidine

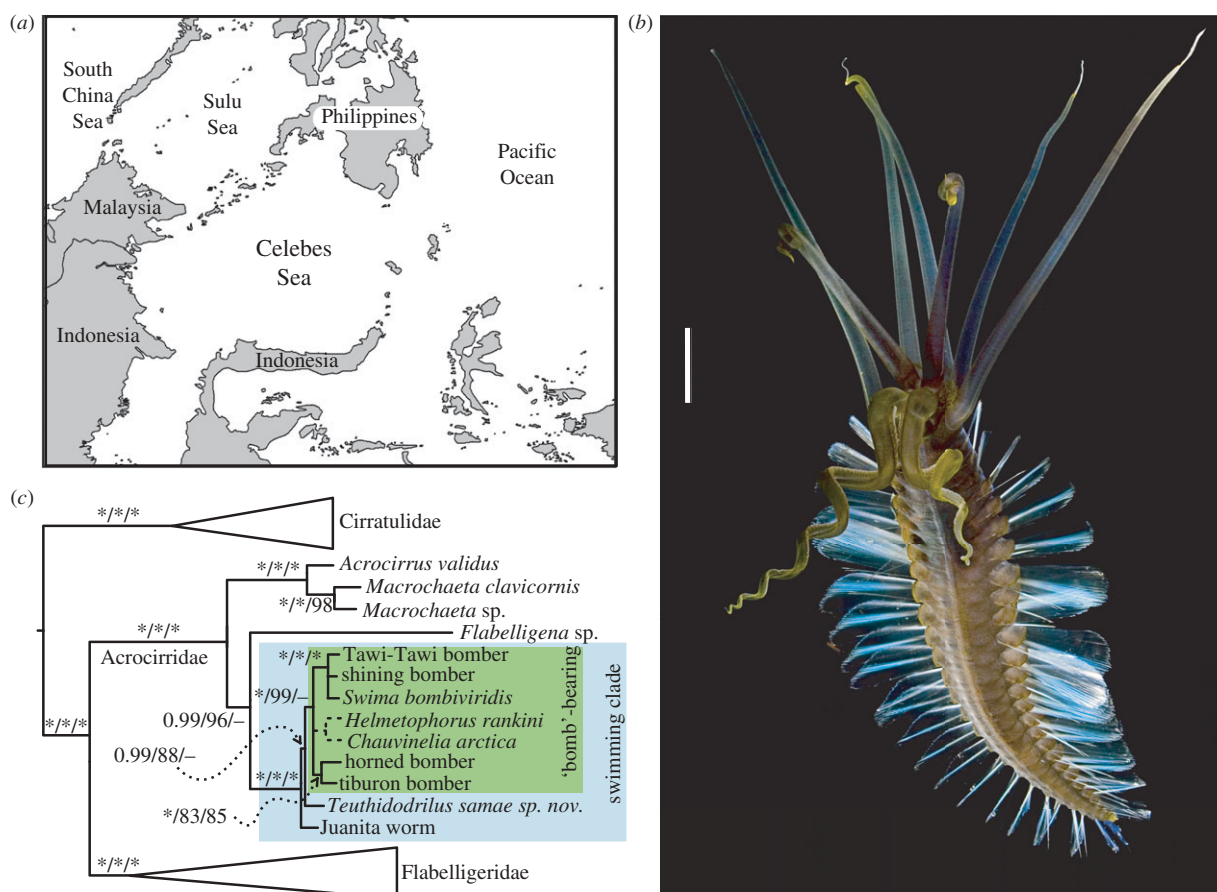


Figure 1. (a) Map of Celebes Sea and surroundings. (b) Ventro-lateral view of live paratype 3 or 4. Photograph, Michael Aw 2007. Scale bar, 15 mm. (c) Simplified version of the tree from Osborn & Rouse [12] showing the phylogenetic position of *T. samae* gen. and sp. nov.

Table 1. *Teuthidodrilus samae* gen. and sp. nov. collection information.

number	accession number	depth (m)	length (mm)		date	locality	number of chaetigers	nuchal shape
			live	fixed				
holotype	NMA 04342	2830	90	65	10 Oct 2007	4°57'43" N, 120°09'42" E	25	smooth
paratype 1	SIO-BIC A2250	approx. 2500–2800	—	38	6 Oct 2007	4°58'00" N, 120°14'36" E	25	smooth
paratype 2	SIO-BIC A2251	2912	20	10+	10 Oct 2007	4°57'43" N, 120°09'42" E	17+	unknown
paratype 3	SIO-BIC A2252	2259	65	60	12 Oct 2007	4°42'37" N, 120°07'30" E	25	smooth
paratype 4	SIO-BIC A2253	2028	94	84	12 Oct 2007	4°42'37" N, 120°07'30" E	32	frilly
paratype 5	MCZ IZ 99582	approx. 2500–2800	—	—	6 Oct 2007	4°58'00" N, 120°14'36" E	—	frilly
paratype 6	MCZ IZ 99583	2039	—	85	10 Oct 2007	4°57'43" N, 120°09'42" E	—	unknown

blue for histological examination. Five genes (*18S*, *28S*, *16S*, *COI* and *CytB*) were sequenced and a 29-character morphological matrix generated and analysed both individually and in combination in order to determine phylogenetic relationships of this and six other recently discovered swimming species to other cirratuliform polychaetes [12].

3. SYSTEMATICS

Teuthidodrilus samae, new genus and species (figures 1b and 2).

Biol. Lett.

(a) *Diagnosis*

A member of Acrocirridae having a pair of grooved palps longer than body. Branchial membrane dorsal, with four pairs of elongate, tapered branchiae equal in length to the body. Nuchal organs as ciliated ridge continuous on six pairs of free-standing, oppositely branched structures. Neuropodia contain two to four simple chaetae, which are flattened in the distal three-quarters. Prominent notopodial lobes contain 50 or more simple, flattened, concavo-convex chaetae

that taper abruptly at the tip forming a fine point. All chaetae with fine rings of tiny spines, most obvious at distal tips. First chaetiger with reduced number of chaetae, and no obvious achaetous anterior segments. Adults with 25 or more chaetigers. Papillae small, clavate, reduced to a single lateral row on the ventrum of each segment and a small longitudinal row between noto- and neuropodial lobes. Gonopores as broad papillae immediately ventral to neuropodia on the second and third chaetigers. Body wall darkly pigmented and gelatinous sheath thin.

(b) *Holotype and paratypes*

The holotype female was collected off Tawi-Tawi, Philippines, October 2007, at 2830 m in 2950 m deep water and is deposited at the National Museum of the Philippines (NMA 04342; table 1). Four paratypes are deposited at the Scripps Institution of Oceanography Benthic Invertebrate Collection (SIO-BIC A2250–A2253) and two are deposited at the Museum of Comparative Zoology, Harvard University (MCZ IZ 99582–99583).

(c) *Brief description of holotype*

Body brown in live specimen, black when preserved. Thin gelatinous sheath. Total preserved body length 65 mm (90 mm before preservation), and body width 10 mm, with 25 chaetigers. Body papillae few, small, clavate.

Prostomium reduced to tissue supporting nuchal organs. Nuchal organs begin anteriorly as a laterally opening, horseshoe-shaped ciliate ridge that continues posteriorly to loop up each major branch of the lateral-most branched free-standing structures, then back down towards the medial line of the head and back, and up each successively more medial pair of free-standing nuchal structures, finally meeting between the medial-most pair of free-standing structures (figure 2*d*, shown in paratype figure 2*a,b*; orange ridge visible in figure 2*h*). Grooved palps frontal, coiled. Mouth antero-ventrally located, pharynx unarmed. Four pairs of elongate, tapered branchiae attached in two rows posterior to the nuchal organs, longest at least 68 mm in length. Anterior nephridiopores as pair of broad-based, darkly pigmented papillae lateral to antero-medial-most branchiae (black dots seen in paratype figure 2*a*).

Chaetigers with prominent notopodia, distinct from neuropodia, supporting greater than 50 chaetae, except the first chaetiger with less than 10. Notochaetae external length up to 15 mm, simple, broad, flattened, concavo-convex paddles tapering abruptly to a fine point at the distal tip; distal-most margins with fine spines in tightly spaced rows. Neuropodial lobes small, rounded projections, supporting two to four simple chaetae with a round cross section at the base that flattens to a fine-tipped, tapered blade distally, with tiny, closely spaced rows of spines along the entire length (figure 2*i*).

Internal anatomy somewhat visible through the partially transparent body of live specimens. Ventrally located double nerve cord with two pairs of fused ganglia per segment. Gut forms three loops within chaetigers 2–6. Heart body present. Large efferent,

afferent and circular vessels supply elongate branchiae, innervation with identical arrangement (figure 2*c*). Single pair anterior nephridia extend back to the fifth chaetiger. Gonads in chaetigers 2–4 consisting of grape-like clusters of variously sized, beige ova, maximum size nearly 1 mm. Septa complete. Detailed description, etymology, ecological information, and discussion of variation between specimens and taxonomic remarks available in the electronic supplementary material.

4. DISCUSSION

The relative inaccessibility of the deep sea has left most of its vast spaces unexplored, so discovery of new species is seldom surprising. The unusual morphology, large size, numerous observations (16 within seven dives), behaviour and phylogenetic position of *T. samae* are however a surprise. How could such an animal evade collection until now? We believe that the immense volume of deep, pelagic habitat, the difficulty of sampling deep demersal communities and *T. samae*'s ability to swim away from towed observational or sampling gear probably all contributed to its long seclusion.

Although currently monotypic, we do not expect the genus to remain so as exploration with submersibles continues in other areas. A similar animal was observed off western India (10°11'80" N, 75°30'80" E) by the submersible *Hercules 7* in October of 2004. That single observation (specimen not collected) was made at 1005 m depth and was recorded by the SERPENT project (<http://archive.serpentproject.com/231/>). Observable differences in swimming behaviour, posture (see video included in the electronic supplementary material), and observation depth (2000–3000) suggest that the Indian Ocean animal may represent a second species of *Teuthiodrilus*.

The numerous *T. samae* observations collected within just a few dives and all within 100 m of the seafloor suggest that this animal is a common member of the deep benthic-pelagic community of the Celebes Sea basin. The video obtained allows speculation on the ecology (a suspension feeder using large aggregates of marine snow) and insight into the mechanics of swimming. This discovery illustrates how much we have to learn about even the large, common inhabitants of deep-pelagic communities.

Special thanks to the science party of *Exploring the Inner Space of the Celebes Sea 2007* who were involved in the ROV operations and collection of polychaete specimens, Russ Hopcroft, Erich Horgan, Bill Hamner and Emory Kristof. Thank you to the captain and crew of the *BRP Hydrographer Presbitero* and the pilots of *Max Rover Global Explorer*, particularly Joe Caba for his superb collection skills. Thanks to Michael Aw for use of his photographs and to Drs Filemon and Mely Romero for liaison with authorities in Tawi-Tawi. Funding was provided to L.P.M. by grants from NOAA's Office of Ocean Exploration and WHOI Ocean Life Institute, with additional support from the National Geographical Society. The University of California President's Postdoctoral Fellowship provided funding to K.J.O. Thanks to Bruce Robison, Fredrik Pleijel

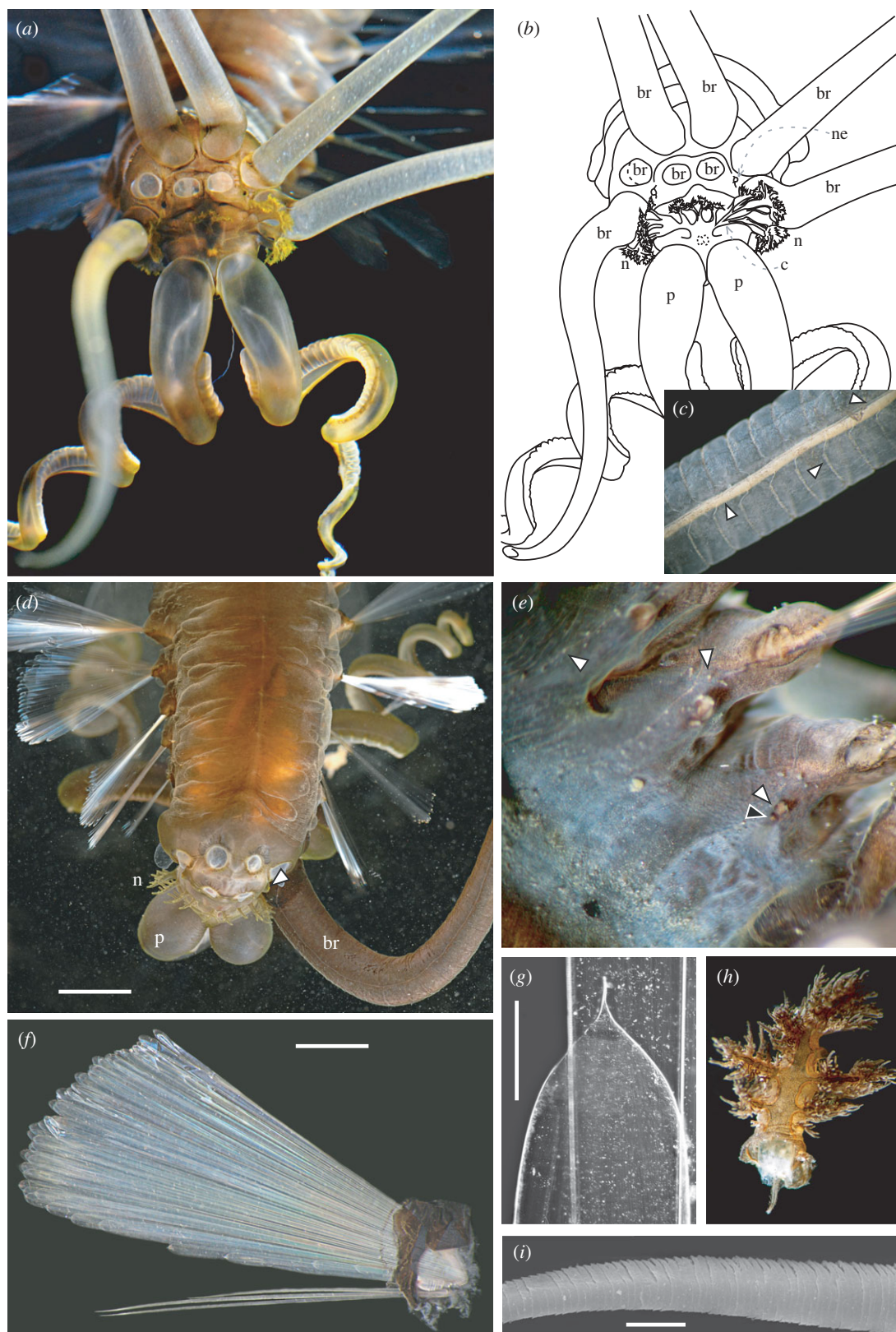


Figure 2. *Teuthidodrilus samae*, gen. and sp. nov. (a and b) Anterior view of paratype 5 showing five attached branchiae (br), nephridiopores (black papillae, ne), branched nuchal organs (n) and the ciliary ridge joining them (c), and palps (p). (c) Shaft of elongate branchia from holotype showing longitudinal vessel (lower arrow), circular vessels (centre arrow) and nerve (upper arrow). (d) Dorsal view of holotype showing attached palps, branchial scars, branched nuchal organs, bubbled remains of the gelatinous sheath and nephridiopore (arrow). (e) Ventral view of paratype 3 showing notopodial (right) and neuropodial lobes (that of third chaetiger, lower white arrow), gonopore (black arrow), row of papillae (top right arrow) between noto- and neuropodial lobes and row of papillae (top left arrow) lateral across ventrum of segment. (f) Parapodium from holotype showing notochaetal fan (top) and neurochaetae (bottom). (g) Tip of notochaeta from holotype; 10 \times magnification is not sufficient to resolve the spinous nature of the distal tip. (h) Dissected free-standing, nuchal structure from paratype 4, frilly. (i) Neurochaeta distal shaft from holotype seen with scanning electron microscopy. Scale bars, $d = 4$ mm, $f = 3$ mm, $g = 0.2$ mm and $i = 10$ μ m. (Online version in colour.)

and Adrian Glover for comments that improved this manuscript and to Linda Kuhnz for assistance with figure 1a.

- 1 Nichols, G. & Hall, R. 1999 History of the Celebes Sea based on its stratigraphic and sedimentological record. *J. Asian Earth Sci.* **17**, 47–59. (doi:10.1016/S0743-9547(98)00034-8)
- 2 Gordon, A., Giulivi, C. F. & Gani Ilahude, A. 2003 Deep topographic barriers within the Indonesian seas. *Deep Sea Res.* **50**, 2205–2228. (doi:10.1016/S0967-0645(03)00053-5)
- 3 Allen, G. R. 2008 Conservation hotspots of biodiversity and endemism for Indo-Pacific coral reef fishes. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **18**, 541–556. (doi:10.1002/aqc.880)
- 4 Robison, B. H. & Hamner, W. M. 2009 *Pocket basins and deep-sea speciation*. In *Encyclopedia of islands* (eds R. Gillespie & D. A. Clague), pp. 755–757. Berkeley, CA: University of California Press.
- 5 Wishner, K. F. 1980 The biomass of the deep-sea benthopelagic plankton. *Deep Sea Res.* **27**, 203–216. (doi:10.1016/0198-0149(80)90012-6)
- 6 Smith, K. L., Kaufmann, R. S., Edelman, J. L. & Baldwin, R. J. 1992 Abyssoplagic fauna in the central North Pacific: comparison of acoustic detection and trawl and bated trap collections to 5800 m. *Deep Sea Res.* **39**, 659–685. (doi:10.1016/0198-0149(92)90094-A)
- 7 Robison, B. R., Sherlock, R. E. & Reisenbichler, K. R. 2010 The bathypelagic community of Monterey Canyon. *Deep Sea Res.* **57**, 1551–1556. (doi:10.1016/j.dsr.2010.02.021)
- 8 Robison, B. H. 2004 Deep pelagic biology. *J. Exp. Mar. Biol. Ecol.* **300**, 253–272. (doi:10.1016/j.jembe.2004.01.012)
- 9 Haddock, S. H. D. 2004 A golden age of gelata: past and future research on planktonic ctenophores and cnidarians. *Hydrobiologia* **530/531**, 549–556. (doi:10.1007/s10750-004-2653-9)
- 10 Vecchione, M. *et al.* 2001 Worldwide observations of remarkable deep-sea squids. *Science* **294**, 2505. (doi:10.1126/science.294.5551.2505)
- 11 Eschmeyer, W. N., Fricke, R., Fong, J. D. & Polack, D. A. 2010 Marine fish diversity: history of knowledge and discovery (Pisces). *Zootaxa* **2525**, 19–50.
- 12 Osborn, K. J. & Rouse, G. W. In press. Phylogenetics of Acrocirridae and Flabelligeridae (Cirratuliformia, Annelida). *Zool. Scr.* (doi:10.1111/j.1463-6409.2010.00460.x)
- 13 Robison, B. H. 1992 Midwater research methods with MBARI's ROV. *Mar. Technol. Soc. J.* **26**, 32–39.

The remarkable Squidworm is an example of discoveries that await in deep-pelagic habitats

Karen J. Osborn, Laurence P. Madin, Greg. W. Rouse

S1. Supplemental Results and Discussion

- (a) *Phylogenetics*
- (b) *Generic-level etymology*
- (c) *Generic-level remarks*
- (d) *Species-level etymology*
- (e) *Complete description of holotype*
- (f) *Variation*
- (g) *Species-level remarks*
- (h) *Ecology and behavior*

S2. Supplemental References

S3. *In situ* video of *Teuthidodrilus samae*

S1. Supplemental Results and Discussion

(a) *Phylogenetics*

All seven recently discovered swimming species formed a clade within Acrocirridae based on sequence data from five genes and a 29 character morphological matrix analyzed separately and in combination with Bayesian, maximum likelihood, and parsimony methods (Figure 1A and [12]). Although genetic data was unavailable for *Helmetophorus* and *Chauvinelia*, morphological data placed them within that clade as well (position indicated by dotted branches Figure 1A). *Teuthidodrilus samae* gen. and sp. nov. was sister to a clade containing all “bomb”-bearing species but distinct from all available acrocirrids and polychaetes. In the parsimony analysis of combined genetic and morphological data, “Juanita worm” and *T. samae* formed a clade but this is likely completely due to the arrangement of their branchiae on a branchial membrane instead of

on individual segments and the possession of free-standing nuchal structures, characters which these taxa share and which differ from all other swimming acrocirrids. These two species formed a clade in no other analyses. These two species also share demersal ecology although Juanita worm was often been observed in contact with the seafloor while *T. samae* has not.

(b) *Generic-level Etymology*

Named for the impression given by this animal, when observed *in situ*, of being a chimera of squid (10 elongate, arm-like appendages) and worm. The Greek roots of teuthid (genitive, squid) and drilos (nominative, worm) are combined to form this masculine generic name.

(c) *Generic-level remarks*

Teuthidodrilus shares presence of body papillae, a subterminal mouth, presence of grooved prostomial palps, branchiae restricted to the anterior region of the body, and a single pair of large anteriorly located nephridia with Flabelligeridae and Acrocirridae.

Teuthidodrilus exhibits the gelatinous sheath, position of the nephridiopores and branchial membrane of a flabelligerid, but possesses the spinous chaetae and non-retractable head of an acrocirrid. The size, shape and length of branchiae, few body papillae, and shape of the notochaetae (broad, flattened, concavo-convex, with abrupt tapering to a fine tip distally) and neurochaetae (simple instead of pseudocompound as is typical of benthic acrocirrids) distinguish *Teuthidodrilus* from all other acrocirrids.

(d) *Species-level Etymology*

Named in honor of the Bangsa Sama people who inhabit the region surrounding the original collection locality. Samae is used in the genitive case as a noun in apposition and is masculine.

(e) *Description of holotype*

All information contained in the print version of this description is repeated within this more detailed description.

Body brown to black (Figure 2D). Thin gelatinous sheath only visible when damaged and bubbled up or as peeling fragments behind peristomium and at chaetal bases (shown in paratype Figure 2E). Total preserved body length 65 mm (90 mm before preservation), body width 10 mm, with 25 chaetigers. Body broadest in anterior third, tapering from this point to unadorned pygidium (shown in paratype Figure 1B). Posterior chaetigers with successively fewer and smaller chaetae, dramatic reduction in the four posterior-most segments. Chaetigers with projecting notopodial and reduced neuropodial rami (Figure 2F). Four (sometimes three or five) clavate, interramal papillae not noticeably larger than other body papillae (shown in paratype Figure 2E). Single rows of small, clavate papillae running laterally on ventrum of each chaetiger, in anterior-most segments papillae visible only as pair on either side of ventral nerve cord (shown in paratype Figure 2E). Similar row of papillae on dorsum of posterior segments.

Head consists of prostomium, with complex nuchal organs, and peristomium, with grooved, coiled palps, branchial membrane, elongate, tapered branchiae, and nephridiopores. Prostomium reduced to tissue posterior to palps that supports the nuchal

organs. Nuchal organs begin anteriorly as laterally opening, horseshoe-shaped ciliate ridge that continues posteriorly to loop up each major branch of the lateral-most free-standing branched structures then back down toward the medial line of the head and back and up each successively more medial pair of free-standing nuchal structures, finally meeting between the medial-most pair of free-standing structures (Figure 2D, shown in paratype Figure 2A, B, H). Nuchal organs highly vascularized, appearing yellow in live animals because of blood visible through epidermis (figure 2D). Grooved frontal palps much longer than body (at least 80 mm after preservation), with epidermal pigmentation of purple to brown, coiling from base. Mouth antero-ventrally located, unarmed, with muscular oral tube, pigmented as the rest of the body. Four pairs of elongate, tapered branchiae attached in 2 rows (anterior row with 1 pair branchiae, posterior row with 3 pairs, shown in paratypes Figure 1B, 2A) posterior to the nuchal organs, longest at least 68 mm in length. *In situ* video observations suggest tips may be thinner filament but all branchiae tips missing or damaged in holotype. Branchial scars consist of thin, transparent tissue that bulges outward (Figure 2D). Nephridiopores single pair of low, broad-based, darkly pigmented papillae lateral to antero-medial-most branchiae (black dots seen in paratype Fig. 2A). Two pair low, clavate papillae on branchial membrane near margins of anterior and posterior medial branchiae.

Chaetigers not differentiated into thoracic and abdominal. Notopodial lobes prominent, distinct from neuropodial lobes (shown in paratype Figure 2E), supporting greater than 50 chaetae (Figure 2F) except first chaetiger with less than 10. Notochaetae simple, concavo-convex from base to abruptly tapered fine tip, tips often broken off, margins of distal portion with fine spines in tightly spaced rows, external length up to 15

mm (Figure 2F, G). Neuropodial lobes small, rounded projections, supporting three (sometimes two or four) simple chaetae with a round cross-section at the base but flatten to a fine tipped, tapered blade, with tiny, closely spaced rows of spines along entire length (Figure 2I). Gonopores as slightly projecting, broad-tipped papillae located just ventral to the neuropodia in chaetigers 2 and 3 (shown in paratype Figure 2E).

Internal anatomy somewhat visible through partially transparent body of live specimens. Ventrally located double nerve cord with two pairs of fused ganglia per segment, diverging just posterior to peristomium to surround the oral apparatus and fusing again in the prostomium just posterior to the palp attachments (Figure 2A, B). The gut is straight through the first chaetiger, then forms 3 loops within chaetigers 2–6 before it continues straight to the pygidium. The anterior gut wall is deeply pigmented appearing completely black. The heart body is a large vessel first visible from the convergence of several vessels in the peristomium and running to the coiled region of the gut. Large efferent and afferent vessels supply elongate branchiae, entering the base of the branchia at a single point and diverging to opposite sides, connected by smaller diameter circular vessels (Figure 2C). Circular vessels give preserved branchiae appearance of being segmented. Two large nerves run length of each branchia, are found just beneath the epidermis, are easily dislodged during handling, and have branches that shadow each circular vessel. A single pair of large nephridia is found from the first chaetiger, folding back to the fifth chaetiger and exiting through the nephridiopores in the branchial membrane. Nephridia contained hundreds of beige spherical bodies measuring 0.25 mm in diameter. Gonads in chaetigers 2–4 consisting of grape-like clusters of variously sized,

beige ova, maximum size nearly 1 mm. Gametes exit the body through the gonopores. Septa complete.

(f) Variation

All specimens with 25 chaetigers (20–85 mm total preserved body length) except paratype 4 (84 mm), which had 32 chaetigers and paratype 2, which was obviously an immature specimen. Single small specimen (paratype 2) was nearly transparent but all others were darkly pigmented over iridescent, broad longitudinal muscle bands.

Palps and branchiae easily lost but large, obvious scars remain. Tips of branchiae with distinctly differentiated region at tip that is highly elastic and narrow compared to breadth of main portion of branchia. Combination of video observation and ruffled appearance of tips suggest they are elastic and extendable.

Freestanding nuchal structures not easily lost. Large specimens with numerous additional side branches (frilly) on the upright portions of the nuchal organs as in Figure 2H that do not support the ciliate ridge but do contain blood vessels. Smaller specimens lacked these numerous side branches and were referred to as smooth (Figure 2D, Table 1).

Chaetigers 2–5 often ruptured due to coiled gut contained therein.

(g) Species-level remarks

Teuthidodrilus is currently a monotypic genus but a similar animal was observed in the northern Indian Ocean. Due to its depth, location, and differences in swimming behavior and posture, is likely a second species. *Teuthidodrilus samae* differs from all other

swimming acrocirrids (members of *Swima*, *Helmetophorus*, *Chauvinelia*, and two other as yet undescribed species) in the shape of its noto- and neurochaetae, the great length of its palps and branchiae, possessing only one form of branchiae, the extent of dark pigmentation on its epidermis, and its size. *Teuthidodrilus samae* is most closely related to an as yet undescribed species of acrocirrid referred to as Juanita worm. The two species differ in that *T. samae* lacks the elongate achaetous anterior segments, possesses branchiae that are nearly as long as the body (while those of Juanita worm are just over half the length of the body), has only oppositely branched, freestanding nuchal organs, has simple neurochaetae, differs in the shape of the noto- and neurochaetae, has prominent nephridiopores on the branchial membrane, differs in the position of the gonopores, and has a more prominent gelatinous sheath.

(h) *Ecology and Behavior*

Teuthidodrilus samae was found off Tawi Tawi, Philippines from 2028–2912 m depth within approximately 100 meters of the seafloor. Individuals were not observed to interact with the seafloor although they were sometimes observed within sight of it. Gut contents of two examined specimens contained fine sediment, but it was not possible to determine if this was obtained from the water column (sinking or resuspended) or directly from the seafloor.

The two examined guts contained what appeared to be soft tissue, fine particulate matter consisting of pelagic phyto- and zooplanktonic skeletons and what may have been fine sediment particles. One individual was observed attached to what appeared to be the collapsed mucus filter of a larvacean or some other large aggregation of marine snow,

which was dislodged from the animal by physical disturbance during collection of the individual. No other observations were made that could be construed as feeding.

Observed *T. samae* were less active and agile than other members of the swimming clade and had a minimal escape response during collection or disturbance (Video supplement) thus it is assumed that they are not predators on active prey but instead likely to be suspension feeders, possibly utilizing the elongate branchiae and palps to collect aggregated marine snow or small, passively drifting prey items.

The vast volume of the deep-pelagic realm and extremely limited reach of the lights and cameras on submersibles make it atypical to see several individuals of the same species on a single dive, or even a single dive series, with the exception of the most abundant species (e.g. *Poebius meseres* or *Vanhoeffenura* sp. of Monterey). We believe this species is fairly abundant because at least one individual was observed per remotely operated vehicle dive, for a total of at least 16 observations in just seven dives.

We believe these are not epitokes of a benthic polychaete. All animals were examined for gonad ripeness and found to be in various stages of gonad development and the gonads occupied only a small proportion of the body even in individuals with large (nearly 1 mm) eggs. Additionally, the animals are large and conspicuous with their darkly pigmented bodies and long head appendages, thus they could be easily distinguished if observed on the seafloor.

Animals were most often observed hanging obliquely or slowly undulating in the water column with elongate branchiae held erect and away from the body. The anterior dorso-medial pair of elongate branchiae was directed anteriorly, while the posterior pair was held at a 30–45° angle back over the dorsum. The ventral-most pair of lateral

elongate branchiae was held at a 30–45° angle down along the ventrum, while the lateral pair was held approximately perpendicular to the body and folded (or draped) posteriorly from near the midpoint of their length. The palps were directed ventrally and the majority of their length kept coiled beneath the body.

Forward and near stationary swimming was observed, but rearward swimming, common in close relatives of the genus (Osborn, unpub.), could not be confirmed from the *in situ* video available. Metachronal waves are generated from posterior to anterior during swimming, resembling that described for *Nereis* by Gray [S1]. Undulation wavelength is long, involving at least ten chaetigers, and presumably generated by antagonistic contraction of the dorso-lateral longitudinal muscle bands. It is assumed that the broad, paddle-like chaetae twist on the recovery stroke to reduce drag as is often observed in drag-based swimming [S2]. Additionally, the cross-sectional profile of the notochaetae is slightly concave posteriorly, which provides rigidity during the power stroke.

S2. Supplemental References

S1. Gray, J. 1939. Studies in animal locomotion VIII. The kinetics of locomotion of *Nereis*

diversicolor. *J. Exp. Biol.* **16**, 9-17.

S2. Wootton, R. J. 1999. Invertebrate paraxial locomotory appendages: design, deformation and

control. *J. Exp. Biol.* **202**, 3333-3345.

S3. *In situ* video of *Teuthidodrilus samae*. Compilation of 5 individual observations including 4 collection events (three with the suction sampler and one collection in the detritus sampler).

Ventral view of animal followed by movement of the vehicle to the right around the animal giving a lateral, then dorsal view. The animal is slowly swimming initially and eventually becomes still. The second collection event (that with the detritus sampler) shows the animal at the time when it was disturbed to the point where it lost the aggregated marine snow it was attached to when it was first observed. The aggregated marine snow breaks apart and swirls around the animal and sampler as the animal comes in contact with the sampler canister.