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***Itheyaspira bathycodon* new genus and species (Vetigastropoda: Trochoidea: Turbinidae: Skeneinae) from the Von Damm Vent Field, Mid-Cayman Spreading Centre, Caribbean**

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Abstract

Itheyaspira bathycodon gen. nov. and sp. nov. is discovered at the Von Damm hydrothermal vent field on the world's deepest spreading centre, the Mid-Cayman Spreading Centre (MCSC), Caribbean, at 2300 m depth. The new species is described and illustrated on the basis of 11 specimens and brief notes on its habitat and known distribution are provided. Molecular phylogenetic data from partial COI mDNA, 16S rDNA and nuclear 18S rDNA regions are used to analyse the species' phylogenetic position and morphological affinities with previously described skeneid and vents genera and species are discussed. The new species is distinguished from the most closely allied vent species, *Itheyaspira lequios* Okutani, Sasaki & Tsuchida, 2000 and *Fucaria mystax* Warén & Bouchet, 2001 at the generic level based on considerable morphological differences in radula diagnosis and appendage structure of the head-foot. In consideration of both the morphological and molecular evidence, the new species is assigned to the subfamily Skeneinae. *T. bathycodon* gen. nov. and sp. nov. is the tenth turbinid to be described from a hydrothermal-vent environment and the second taxon to be described from recently discovered hydrothermal vents on the MCSC. The characterisation of faunal assemblages at MCSC vents has the potential to elucidate the factors determining vent biogeography of this region.

Key words: Gastropoda, Vetigastropoda, Trochoidea, Turbinidae, Skeneinae, *Itheyaspira*, *bathycodon*, new genus, new species, Cayman, hydrothermal vents.

INTRODUCTION

Gastropoda are the most species-rich group of described vent macrofauna (Warén et al., 2006), and they are a dominant component of the faunal assemblages at vent sites in the western Pacific and on the Central- and Southwest-Indian Ridges (e.g. Desbruyères et al., 1994; Galkin, 1997; Kojima et al., 2001; Van Dover et al., 2001; Tao et al., 2011). A substantial research effort has sought to elucidate the systematics and higher phylogeny of vent/seep gastropods, and to characterise their diversity, biogeography and life-history biology (see Sasaki et al., 2010 for recent review).

More than 200 species of gastropods from over 100 genera and more than 35 families have been described from deep-sea chemosynthetic environments in all the world's oceans (Sasaki et al., 2010). While some of those species also inhabit non-chemosynthetic environments but have been recorded in much greater densities from

chemosynthetic assemblages (see Sasaki et al., 2010), others are endemic at the species and higher taxonomic levels (e.g. Warén & Bouchet, 2001).

The subfamily Skeneinae Clark, 1851 was traditionally treated as a separate family (“Skeneidae”) in Trochoidea Rafinesque, 1815 (e.g. Hickman & McLean, 1990). More recent anatomical and molecular studies showed however that “Skeneidae” was polyphyletic and that many genera should be reassigned (e.g. Bouchet et al. 2005, Kano, 2008). Bouchet et al. (2005) were the first to rank Skeneinae as a subfamily of the Turbinidae Rafinesque, 1815, an arrangement maintained by Williams et al. (2008) in the newly-defined Turbinidae. To date, all turbinids endemic to deep-sea chemosynthetic environments belong to either Skeneinae or Margaritinae Thiele, 1924 (Sasaki et al., 2010; see Table 1).

The Von Damm Vent Field (VDVF) is an active, high-temperature hydrothermal system, situated in a unique off-axis setting on the upper slopes of an oceanic core complex at 2300 m depth (Connelly et al., 2012). The VDVF supports an abundant faunal assemblage that is dominated by dense aggregations of the shrimp *Rimicaris hybisae* Nye, Copley & Plouviez, 2012 and includes small skeneimorph gastropods. During a recent cruise to the Caribbean Mid-Cayman Spreading Centre a piece of sulphide chimney was sampled from the VDVF. On the surface of the sampled sulphide chimney were several small gastropods of one species, *Iheyaspira bathycodon* gen. nov. and sp. nov., which is described herein and assigned to the subfamily Skeneinae. In addition to enhancing existing knowledge of biodiversity, characterising the members of the faunal assemblage at MCSC vents has the potential to elucidate the factors determining vent biogeography of this region.

MATERIAL AND METHODS

The gastropods were collected from the Von Damm Vent Field (VDVF, 2300 m) on the Mid-Cayman Spreading Centre, Caribbean, during the 44th voyage of *RRS James Cook* (April 2010). All specimens were picked from the surface of a sample of sulphide chimney, collected by a grab attached to the manoeuvrable TV grab HyBIS (Hydraulic Benthic Interactive Sampler). Specimens for molecular analysis were immediately placed in 100% ethanol and the shell and operculum were subsequently removed. Specimens for morphological study were fixed in 10 % neutralised formalin, subsequently transferred to 90% Industrial Methylated Spirits and measured to the nearest 0.1 mm using Vernier callipers (see Table 2).

Specimen [insert catalogue number] was dissected for scanning electron microscopy (SEM) of shell, operculum and radula. The shell and operculum were bathed in washing-up liquid diluted with water and placed in an ultrasonic cleaning bath for three minutes. The mantle tissue was dissolved in potassium hydroxide diluted in water to expose the radula. Material was mounted uncoated onto an aluminium stub and micrographs were taken with a Hitachi TM3000 tabletop microscope. For SEM of the soft parts, specimen [insert catalogue number] was dehydrated through a graded ethanol series, critical point dried and sputter coated with gold palladium prior to examination with a FEI Quanta 200 Scanning Electron Microscope at accelerating voltage of 10 kV.

Genomic DNA was extracted from xxx specimens using the CTAB (cetyltrimethyl ammonium bromide) extraction procedure (Doyle & Dickson, 1987). A region of mitochondrial cytochrome oxidase subunit I gene (COI) was amplified by polymerase chain reaction (PCR) performed in 20 µl final volume using universal primers (Folmer et al., 1994) and the following conditions: 1X buffer reagent (200 mM Tris

pH 8.8, 500 mM KCl, 0.1 % Triton X-100, 2 mg/ml Bovine Serum Albumen), 2 mM MgCl₂, 0.2 mM of each dNTP, 0.5 mM of each primer, 1 U Taq DNA polymerase (Bioline), 5 µl of template DNA and sterile H₂O to final volume. Thermal cycling conditions were: 94°C/2 min; followed by 5 cycles at (94°C/35 s; 45°C/35 s; 72°C/1:20 min) and 35 cycles at (94°C/35 s; 50°C/35 s; 72°C/1:20 min) with a final extension of 72°C/ 10 min.

For the 16S ribosomal DNA gene (16S), PCR amplifications were performed in 20 µl final volume using 16Sar and 16Sbr primers (Palumbi, 1996) and the following conditions: 1X buffer reagent (same as for COI), 2.5 mM MgCl₂, 0.13 mM of each dNTP, 0.38 mM of each primer, 1 U Taq DNA polymerase (Bioline), 2.5 µl of template DNA and sterile H₂O to final volume. Thermal cycling conditions were: 94°C/4 min; 30 cycles at (94°C/30 s; 52°C/1 min; 72°C/2 min) and 72°C/5 min.

PCR amplifications of the 18S ribosomal DNA gene (18S) were performed using the primer pair 5' -CACAGTGAAACTGCGAATGG-3' and 5' -CAAATGCTTTCGCTGTAGGG-3' (reference of primers required) in a 20 µl final volume amplification mixture as described for COI. Thermal cycling conditions were: 95°C/5 min followed by 30 cycles at (94°C/1 min; 60°C/1 min; 72°C/2 min; 72°C/2 min).

Purifications and sequencing were performed as described by Nye et al. (2012). Sequence strands were proof read and assembled with CodonCode Aligner, version 3.7.1 (CodonCode Corporation, Dedham, MA, USA), to produce a continuous fragment. The 16S and 18S partial rDNA sequences were compared with those of other gastropods available in GenBank using the BLAST program (NCBI Basic Alignment Search Tool). The COI partial sequence of the new species was also compared with those of other trochoids of Suzanne William's published and unpublished dataset of deep-sea gastropods (Williams et al 2008, personal communication). Phylogenetic trees were constructed with MEGA5 (Tamura et al., 2011) using both maximum-likelihood (ML) (Kimura, 1980) and neighbour-joining (NJ) (Saitou & Nei, 1987) methods on 425- and 803-base pair (bp) alignments for 16S and 18S respectively. Bootstrap values were calculated on 1000 re-sampling replicates.

The GenBank accession numbers for the partial sequences of COI, 16S and 18S regions from the new species are JQ306326, JQ306327 and JQ306328 respectively.

SYSTEMATICS

Order VETIGASTROPODA Salvini-Plawen, 1980

Superfamily TROCHOIDEA Rafinesque, 1815

Family TURBINIDAE Rafinesque, 1815

Subfamily SKENEINAE Clark, 1851

Itheyaspira gen. nov. Nye, 2012

DIAGNOSIS

Shell skeneiform, height greater than width, with open and deep umbilicus. Eystalks reduced, eyes absent. Cephalic lappets absent. Right neck lobe divided into three tentacles; left neck lobe single. Five pairs of epipodial tentacle; anterior three pairs juxtaposed, first and third densely papillate; fourth and fifth isolated from first three, densely papillate. Ctenidium monopectinate. Radula rhipidoglossate with the formula $\infty + 9 + 1 + 9 + \infty$ (>20).

TYPE SPECIES

Itheyaspira bathycodon sp. nov.

ETYMOLOGY

The new genus is named after Professor Paul Tyler, in recognition of his outstanding contribution to deep-sea biology.

REMARKS

See “Comparative Remarks” in the description of the new species for comparison with other genera. *Itheyaspira* gen. nov. is included here in the subfamily Skeneinae for reasons addressed in the discussion.

Itheyaspira bathycodon sp. nov. Nye, 2012
(Figures 1-5)

TYPE MATERIAL

Holotype and paratypes deposited in the Natural History Museum, UK (NHMUK) [insert catalogue numbers]. All type material collected from the Von Damm Vent Field, Mid-Cayman Spreading Centre, Caribbean (18° 22.605' N 81° 47.875' W), at 2300 m depth.

DESCRIPTION

Shell (Figure 1). Rounded, skeneiform, sturdy, height greater than width (see Table 2); maximum dimensions 7.2 mm height, 6.1 mm width [insert catalogue no.]. Surface smooth, lacking pigmentation, with thin, beige-white periostracum. Surface and apical region, including the protoconch and early teleoconch, are corroded in most specimens. Protoconch diameter 503 µm in the holotype [insert catalogue no.]. Teleoconch whorls more than 2.5 in number, body whorl large. No nacre or lustre visible on exterior or interior of the shell. Umbilicus open and deep, clearly visible in basal view. Peristome smooth. Aperture large and circular with smooth outer lip.

Operculum (Figure 2A). Moderately thin, corneous, and yellowish-brown; multispiral with a central nucleus and short growing edge, with a good fit to the aperture. Opercula retraction is deep.

Soft parts (Figures 3-5). Animal pale white in colour. Head quite large, snout cylindrical, terminating in a broad tip with mouth positioned at the midline. One pair of cephalic tentacles of similar size to each other and equal in length to the snout; cephalic tentacles densely papillated with what appear to be sensory papillae. Eyestalks subequal in length and width to cephalic tentacles, without visible papillae and eyes. Right eyestalk approximately one-half length of right cephalic tentacle, left eyestalk approximately one-third length of left cephalic tentacle. Cephalic lappets absent. Neck lobes arise from both basal sides of the head. Right neck lobe divided into elongate anterior (RNL1) and posterior (RNL2, RNL3) tentacles. Left neck lobe composed of at least one undivided tentacle beneath the left eyestalk. Foot equipped with five epipodial tentacles on both sides. Right side: first, second and third epipodial tentacles clustered together, similar in size, with dense papillae except on second; fourth and fifth isolated from first three in middle part of epipodium between lobes of epipodial skirt, densely papillate. Left side: first, second and third epipodial tentacles clustered together; first and third epipodial tentacles of similar size with

dense papillae; second slightly smaller, without visible papillae; fourth and fifth isolated from first three in middle part of epipodium, densely papillate. Ctenidium monopectinate, attached along its whole length, with bursicles.

Radula (Figure 2B-D). Rhipidoglossate, bilaterally symmetrical, with the formula $\infty - 9 - 1 - 9 - \infty$ (>20). Length ~ 3.1 mm, width ~ 384 μm , with at least 60 transverse rows along total length in paratype 08 [insert catalogue no.]. Central tooth differentiated in form from lateral teeth; smooth-sided, bell-shaped, wider proximally than distally, with a single incurved central cusp. Lateral teeth of similar size to central tooth, increasing in size outwards; with a long, rounded single central cusp, and an outer apical margin with several flanking denticles (>7); dentition attenuates towards the cusp and is strongest on the outermost lateral. Marginal teeth exceed twenty in number on both sides; cutting plate concave, terminating in a single short cusp; apical margins oblique, each with about 10-14 denticles that are longer and finer than those on the lateral teeth. Outermost marginal teeth in a row are smaller, with weaker dentition and straighter shafts. Marginal rows overlap each other.

No jaws are present.

COMPARATIVE REMARKS

The shell of *Iheyaspira bathycodon* gen. nov. and sp. nov. is superficially similar to that of several other skeneimorph taxa, although the radula pattern is, to our knowledge, unique in both number of teeth and shape.

The new species exhibits morphological affinities with *Iheyaspira lequios* Okutani, Sasaki & Tsuchida, 2000 (Turbinidae: Skeneinae), the type species of a monospecific genus. Affinities with *I. lequios* include conchological similarity and shared radula characters, most notably in the shape of the central tooth (see Okutani et al., 2000: Figure 2, p. 269). The new species does however exhibit several important dissimilarities to *I. lequios*: (1) Shell: small (max. 7.2 x 6.1 mm) rather than minute (max. 5.7 x 5.4 mm in *I. lequios*), umbilicate, teleoconch with more than two whorls; (2) Radula: central tooth bell-shaped, not rhombic/arrow-shaped; only nine (not twelve) pairs of lateral teeth; (3) Eyestalks: reduced, subequal in length and width to cephalic tentacles, as opposed to well-developed, thicker than cephalic tentacles; (4) Neck lobes: right neck lobe composed of three (not two) tentacles; (5) Epipodial tentacles: five (not four) on both sides; left ET1 and ET3 densely papillate (*I. lequios* ET1-3 lack papillae).

The new species is also comparable with the turbinid *Fucaria mystax* Warén & Bouchet, 2001 (Skeneinae), based on similarities in shell and radula characters, especially the shape of the central tooth (see Warén & Bouchet, 2001: Figure 11C, p. 135). *Iheyaspira bathycodon* gen. nov. and sp. nov. is differentiated from *F. mystax* by: (1) Shell: umbilicus clearly visible in basal view, teleoconch with greater number of whorls (>2.5); (2) Radula: central tooth bell-shaped, lacking drawn out and narrow anterior support; only nine (not eleven) pairs of lateral teeth; (3) Eye stalks: do not encircle cephalic tentacles.

Despite some similarities of *Iheyaspira bathycodon* gen. nov. and sp. nov. with both *Iheyaspira lequios* and *Fucaria mystax*, the new species is distinguished at the genus level based on striking differences in the radula and appendage structure of the head-foot. Moreover, members of the genus *Fucaria* Warén & Bouchet, 1993 are equipped with a coat of sensory papillae on the snout, a feature not observed in the new species.

DISTRIBUTION & HABITAT

Known only from the type locality, the Von Damm Vent Field, Mid-Cayman Spreading Centre, Caribbean in 2300m depth. See Connelly et al. (2012) for a description of the VDFV geological, geochemical and biological settings.

ETYMOLOGY

The species name *bathycodon* is derived from the Greek words for deep and bell, in reverence to the species' deep-sea habitat and bell-shaped rachidian tooth.

MOLECULAR PHYLOGENY

Partial sequences of the COI (549 bp), 16S (505 bp) and 18S (803 bp) region of *Iheyaspira bathycodon* gen. nov. and sp. nov. were consistent amongst specimens. Fixed and unique mutations were observed in the partial sequences of the COI, 16S and 18S regions. When compared with partial sequences of COI in the gastropod dataset of Suzanne Williams (NHMUK) the partial COI sequence of the new species was near other trochoidean skeneimorph taxa and unique amongst any of the species available (Suzanne Williams, pers. com.). Based on a 425-bp alignment of partial 16S sequences, NJ and ML phylogenetic trees place the new species in the same clade (Turbinidae: Skeneinae) as *Dillwynella* cf. *vitrea* [AY163406.1], *Protolira valvatooides* [AY163405.1] and *Protolira* sp. [GQ160698.1], with 96% and 87% bootstrap support for NJ and ML methods respectively (Figure 6). Of the 16S partial sequences available in GenBank the new species is closest in evolutionary distance to *D. cf. vitrea* (14% divergence). Phylogenetic analyses on an 803-bp alignment of partial 18S sequences of turbinid species place the new species closest in evolutionary distance to *D. planorbis* [AB365310.1], with 39% and 42% bootstrap support for NJ and ML methods respectively. The new species exhibits 1.4% divergence from *D. planorbis* across an 803 bp of the 18S region.

DISCUSSION

The comprehensive molecular and morphology studies on the specimens of an unknown trochoid gastropod have revealed the presence of a new genus and species.

The presence of unique and fixed mutations in the partial sequences of the COI, 16S and 18S regions suggest that *Iheyaspira bathycodon* gen. nov. and sp. nov. is genetically distinct from all other genera and species in the GenBank database. This supports indications based on morphology that *T. bathycodon* is a new genus and new species. Partial sequences of the COI, 16S and 18S regions were consistent between specimens, confirming that the specimens analysed are the same species.

The morphology of the new species is most closely allied to *Iheyaspira lequios* and *Fucaria mystax* (see above), both of which are known only from hydrothermal vents in the Pacific at water depths less than 1500 m (see Table 1). It is, however, excluded from both genera by striking differences in the radula and appendage structure of the head-foot (see above).

The systematic position of both *Iheyaspira* and *Fucaria* is uncertain because there are no sequences available in GenBank for either genus; however both genera are classified currently within the family Turbinidae and subfamily Skeneinae (e.g. Bouchet, 2010 a, b; Sasaki et al., 2010). After redefining the Turbinidae, Williams et al. (2008) remarked that it is hard to determine morphological characters that are typical of this family, and even suggested that the Skeneinae could be considered as a group distinct from (but most closely related to) Turbinidae (Williams et al., 2008). Morphological features of the Skeneinae shared with the new species include the

monopectinate ctenidium and absence of any visible nacre. In addition, the shell of the new species bears superficial resemblance to that of other members of the Skeneinae, such as *Protolira* spp. In the GenBank database sequences for the Skeneinae are available presently for a few species only. Despite this impediment, comparative 16S results presented herein suggest the proximity of the new species to members of the Skeneinae, with strong bootstrap support for inclusion of the new species within this clade. This is further supported by comparative 18S results, whereby NJ and ML methods both place the new species closest in evolutionary distance to *Dillwynella planorbis* [AB365310.1], although this is with weak bootstrap support (39% and 42% for NJ and ML methods respectively). Based on the morphological evidence and current position of *Iheyaspira* and *Fucaria*, and supported by the results from molecular analyses, *Iheyaspira bathycodon* gen. nov. and sp. nov. is assigned to the subfamily Skeneinae.

The first right neck lobe tentacle (RNL1) in the new species may be modified (see Figure xx). Warén & Bouchet (1989) described a modified neck lobe tentacle in *Bathymargarites symplector* Warén & Bouchet 1989 and interpreted this modified appendage as a penis. Collection of further specimens will enable the reproductive anatomy of the new genus and species to be characterised.

The recent discovery of hydrothermal vents and chemosynthetic assemblages on the MCSC has provided an opportunity to enhance existing knowledge of biodiversity in the deep sea. *Iheyaspira bathycodon* gen. nov. and sp. nov. is the first new genus and second new species to be described from the VDVF, and the tenth turbinid gastropod to be described from a hydrothermal vent environment to date (Table 1). Further characterisation of the faunal assemblage at MCSC vents, requiring the collection of other taxa on future research cruises, has the potential to elucidate the factors determining vent biogeography of this region.

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REFERENCES

- Bouchet P.** (2010a). *Itheyaspira* Okutani, Sasaki & Tsuchida, 2000. In: Bouchet, P.; Gofas, S.; Rosenberg, G. (2010) World Marine Mollusca database. Accessed through: World Register of Marine Species at <http://www.marinespecies.org/aphia.php?p=taxdetails&id=456431> on 2011-12-17
- Bouchet P.** (2010b). *Fucaria* Warén & Bouchet, 1993. In: Bouchet, P.; Gofas, S.; Rosenberg, G. (2010) World Marine Mollusca database. Accessed through: World Register of Marine Species at <http://www.marinespecies.org/aphia.php?p=taxdetails&id=456416> on 2011-12-17
- Bouchet P., Racroi J.P., Fryda J., Hausdorf B., Ponder W., Valdes A. & Warén A.** (2005) Classification and nomenclature of gastropod families. *Malacologia* 47, 1-368.
- Clark W.** (1851) On the classification of the British marine testaceous Mollusca. *Annals and Magazine of Natural History* 2, 469-482.
- Coleman C.O.** (2003) "Digital inking": How to make perfect line drawings on computers. *Organisms Diversity & Evolution* 3, Electronic Supplement 14, 1-14.
- Connelly D.P., Copley J.T., Murton B.J., Stansfield K., Tyler P.A., German C.R., Van Dover C.L., Amon D., Furlong M., Grindlay N., Hayman N., Hühnerbach V., Judge M., Le Bas T., McPhail S., Meier, A., Nakamura K-I, Nye V., Pebody M., Pedersen R.B., Plouviez S., Sands C., Searle R.C., Taws S. & Wilcox S.** (2012) Hydrothermal vent fields and chemosynthetic biota on the world's deepest seafloor spreading centre. *Nature Communications* doi: 10.1038/ncomms1636.
- Dall W.H.** (1889) Reports on the results of dredgings, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877-78) and in the Caribbean Sea (1879-80), by the U. S. Coast Survey Steamer "Blake". *Bulletin of the Museum of Comparative Zoology* 18, 1-492.
- Desbruyères D., Alayse-Danet A.-M., Ohta S. & the Scientific Parties of BIOLAU and STARMER Cruises** (1994) *Marine Geology* 116, 227-242.
- Doyle J.J. & Dickson E.** (1987) Preservation of plant samples from DNA restriction endonuclease analysis. *Taxon* 36, 715-722.
- Fabri M.-C., Bargain A., Briand P., Gebruk A., Fouquet Y., Morineaux M. & Desbruyères D.** (2011) The hydrothermal vent community of a new deep-sea field, Ahasze-1, 12°58'N on the Mid-Atlantic Ridge. *Journal of the Marine Biological Association of the United Kingdom* 91, 1-13.
- Folmer O., Black M., Hoeh W., Lutz R. & Vrijenhoek R.** (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3, 294-299.
- Galkin S. V.** (1997). Megafauna associated with hydrothermal vents in the Manus Back-Arc Basin (Bismarck Sea). *Marine Geology* 142, 197-206.

- Hickman C.S. & McLean J.H.** (1990) Systematic revision and suprageneric classification of Trochacean gastropods. *Natural History Museum of Los Angeles County Science Series* 35, 1-77.
- Jukes T.H. & Cantor C.R.** (1969) Evolution of protein molecules. In Munro H.N., (ed) *Mammalian Protein Metabolism*. New York: Academic Press, pp. 21–132.
- Kano Y.** (2008) Vetigastropod phylogeny and a new concept of Seguenzioidea: independent evolution of copulatory organs in the deep-sea habitats. *Zoologica Scripta* 37, 1-21.
- Kiel S.** (2004) Shell structures of selected gastropods from hydrothermal vents and seeps. *Malacologia* 46, 169-183.
- Kimura M.** (1980) A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* 16, 111–120.
- Kojima S., Segawa R., Fujiwara Y., Fujikura K., Ohta S. & Hashimoto J.** (2001) Phylogeny of hydrothermal-vent endemic gastropods *Alvinoconcha* spp. from the western Pacific revealed by mitochondrial DNA sequences. *Biological Bulletin* 200, 298-304.
- Nye V., Copley J. & Plouviez S.** (2012) A new species of *Rimicaris* (Crustacea: Decapoda: Caridea: Alvinocarididae) from hydrothermal vent fields on the Mid-Cayman Spreading Centre, Caribbean. *Journal of the Marine Biological Association of the United Kingdom*, doi:10.1017/S0025315411002001. [ADD PRINT DETAILS](#)
- Okutani T., Tsuchida E., & Fujikura K.** (1992) Five bathyal gastropods living within or near the *Calypptogena* community of the Hatsushima Islet, Sagami Bay. *Venus* 51, 137-148.
- Okutani T., Sasaki T. & Tsuchida T.** (2000) Two additional new species to gastropod fauna of chemosynthetic site on North Knoll of Iheya Ridge, Okinawa Trough. *Venus* 59, 267-275.
- Okutani T., Hashimoto J. & Sasaki T.** (2004) New gastropod taxa from hydrothermal vent (Kairei Field) in the central Indian Ocean. *Venus* 63, 1-11.
- Rafinesque C.S.** (1815) *Analyse de la nature ou tableau de l'univers et des corps organisés*. Palermo: L'Imprimerie de Jean Barravecchia.
- Saitou N. & Nei M.** (1987) The neighbour-joining method: A new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution* 4, 406–425.
- Salvini-Plawen L.v.** (1980) A reconsideration of systematics in the Mollusca (Phylogeny and higher classification). *Malacologia* 19, 249-278.

- Sasaki T., Okuntani T. & Fujikura K.** (2005) Molluscs from hydrothermal vents and cold Seeps in Japan: A review of taxa recorded in twenty recent years (1984-2004). *Venus* 64, 97-133.
- Sasaki T., Warén A. , Kano Y., Okutani T. & Fujikura K.** (2010) Gastropods from recent hot vents and cold seeps: Systematics, diversity and life strategies. *Topics in Geobiology* 33, 169-254.
- Tamura K., Peterson D., Peterson N., Stecher G., Nei M., and Kumar S.** (2011) MEGA5: Molecular Evolutionary Genetics Analysis using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Methods. *Molecular Biology and Evolution*, doi:10.1093/molbev/msr121.
- Tao C., Lin J., Guo S., Chen Y.J., Wu G., Han X., German C.R., Yoerger D.R., Zhou N., Li H., Su X., and the DY115-19 (Legs 1-2) and DY115-20 (Legs 4-7) Science Parties** (2011) First active hydrothermal vents on an ultraslow-spreading center: Southwest Indian Ridge. *Geology* doi: 10.1130/G32389.1
- Thiel J.** (1924) *Handbuch der Zoologie 5, Mollusca*. Berlin: Walter de Gruyter.
- Van Dover C.L., Humphris S.E., Fornari D., Cavanaugh C.M., Collier R., Goffredi S.K., Hashimoto J., Lilley M.D., Reysenbach A.L., Shank T.M., Von Damm K.L., Banta A., Gallant R.M., Gotz D., Green D., Hall J., Harmer T.L., Hurtado L.A., Johnson P., McKiness Z.P., Meredith C., Olson E., Pan I.L., Turnipseed M., Won Y., Young C.R. & Vrijenhoek R.C.** (2001) Biogeography and ecological setting of Indian Ocean hydrothermal vents. *Science* 294, 818-823.
- Vilvens C. & Sellanes J.** (2006) Descriptions of *Otukaia crustulum* new species (Gastropoda: Trochoidea: Calliostomatidae) and *Margarites huloti* new species (Gastropoda: Trochoidea: Trochidae) from a methane seep area off Chile. *The Nautilus* 120, 15-20.
- Warén A.** (1996) New and little known Mollusca from Iceland and Scandinavia, part 3. *Sarsia* 81, 197-245.
- Warén A. & Bouchet P.** (1989) New gastropods from East Pacific hydrothermal vents. *Zoologica Scripta* 18, 67-102.
- Warén A. & Bouchet P.** (1993) New records, species, genera and a new family of gastropods from hydrothermal vents and hydrocarbon cold seeps. *Zoologica Scripta* 22, 1-90.
- Warén A. & Bouchet P.** (2001) Gastropoda and Monoplacophora from hydrothermal vents and seeps: new taxa and records. *Veliger* 44, 116-231.
- Warén A., Bouchet P. & von Cosel, R.** (2006) Gastropoda. In: Desbruyères D., Segonzac M. & Bright M. (eds) *Handbook of deep-sea hydrothermal vent fauna*. Vienna: Biologiezentrum der Oberösterreichische Landesmuseen, pp. 82-140.

Williams S.T., Karube S. & Ozawa T. (2008) Molecular systematics of Vetigastropoda: Trochidae, turbinidae and trochoidea redefined. *Zoologica Scripta* 37, 483-506.

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FIGURE LEGENDS

Fig. 1. *Iheyaspira bathycodon* gen. nov. and sp. nov., shell, from the Von Damm Vent Field, Mid-Cayman Spreading Centre, Caribbean, 2300 m. A, Holotype [insert catalogue no.]; B, Holotype, lateral view [insert catalogue no.]; C, Holotype, basal view [insert catalogue no.]; D, Paratype, basal view [insert catalogue no.]; E, Holotype, apical view [insert catalogue no.]; F, Holotype, protoconch [insert catalogue number]. **Scale bars to be added. Add arrows to show protoconch.**

Fig. 2. *Iheyaspira bathycodon* gen. nov. and sp. nov., paratype 08 [insert catalogue no] from the Von Damm Vent Field, Mid-Cayman Spreading Centre, Caribbean, 2300 m. A, Operculum; B-C, Radula. **Scale bars to be added.**

Fig. 3. *Iheyaspira bathycodon* gen. nov. and sp. nov., paratype 02 [insert catalogue no] from the Von Damm Vent Field, Mid-Cayman Spreading Centre, Caribbean, 2300 m. SEM micrographs of head-foot. A, Dorsal view; B, Anterior view; C, Right side, lateral view; D, Left side, anterolateral view. **Scale bars to be added. Add labels and abbreviations used.**

Fig. 4. *Iheyaspira bathycodon* gen. nov. and sp. nov., paratype 02 [insert catalogue no] from the Von Damm Vent Field, Mid-Cayman Spreading Centre, Caribbean, 2300 m. SEM micrographs of head-foot, right side. A, **Scale bars to be added. Add labels and abbreviations used.**

Fig. 5. *Iheyaspira bathycodon* gen. nov. and sp. nov., paratype 02 [insert catalogue no] from the Von Damm Vent Field, Mid-Cayman Spreading Centre, Caribbean, 2300 m. SEM micrographs of head-foot, left side. **Scale bars to be added. Add labels and abbreviations used.**

Fig. 6. Neighbour-joining tree of turbinid gastropods based on a 425-bp alignment of partial nucleotide sequences from the mitochondrial 16S region with *Buccinum tenuissimum* (Caenogastropoda: Neogastropoda: Buccinoidea: Buccinidae) as outgroup. Evolutionary distances computed using the Jukes-Cantor method (Jukes & Cantor, 1969) are represented by branch length; scale bar is proportional to inferred nucleotide divergence. Bootstrap support calculated on 1000 re-sampling replicates is shown by the numbers along the branches (NJ, plain text; ML, italic text). GenBank accession numbers are given after species names. **Add GenBank number to new species**

Table 1. Turbinid gastropods described from extant hydrothermal vents/cold seeps up to the end of 2011 (confirmed locations and fully described species only).

Subfamily	Species	Site(s)	Depth (m)	Habitat	Primary references
Margaritinae	<i>Gaza fisheri</i>	GoM: Louisiana Slope; Caribbean Sea: off St Lucia	600-1061	seep	Dall, 1889; Warén & Bouchet, 1993, 2001
	<i>Margarites huloti</i>	Off Central Chile (36°S)	843-728	seep	Vilvens & Sellanes, 2006
	<i>Margarites ryukyensis</i>	OT: North knoll of Iheya Ridge	968-1053	vent	Okutani, Sasaki & Tsuchida, 2000; Sasaki et al., 2005
	<i>Margarites shinkai</i>	OT; SB	1110-1340	vent/seep	Okutani, Tsuchida & Fujikura, 1992; Okutani et al., 1992, 1993; Sasaki et al., 2005
Skeneinae	<i>Bruceiella athlia</i>	Aleutian Trench	Ca. 4800	seep	Warén & Bouchet, 2001; Kiel, 2004
	<i>Bruceiella globulus</i>	LB; NFB	1750-2443	vent	Warén & Bouchet, 1993, 2001; Warén et al., 2006
	<i>Bruceiella wareni</i>	CIR: Kairei	2422-2443	vent	Okutani, Hashimoto & Sasaki, 2004
	<i>Fucaria mystax</i>	Edison Seamount	1483	vent	Warén & Bouchet, 2001; Warén et al., 2006
	<i>Fucaria striata</i>	JdFR: Middle Valley	2425	vent	Warén & Bouchet, 1993; Warén & Bouchet, 2001; Warén et al., 2006
	<i>Iheyaspira lequios</i>	OT: North knoll of Iheya Ridge	968-1053	vent	Okutani, Sasaki & Tsuchida, 2000
	<i>Protolira thorvaldssoni</i>	MAR: Menez Gwen to Snake Pit & Ashadze; off south-western Iceland	850-4080	vents & whale bone	Warén, 1996; Warén & Bouchet, 2001; Warén et al., 2006; Fabri et al., 2011
	<i>Protolira valvatooides</i>	MAR: Menez Gwen to Lucky Strike, Snake Pit	850-3478	vent	Warén & Bouchet, 1993, 2001; Warén et al., 2006
	<i>Iheyaspira bathycodon</i> gen. nov. and sp. nov.	MCSC: Von Damm	2300	vent	This paper

CIR, Central-Indian Ridge; GoM, Gulf of Mexico; JdFR, Juan de Fuca Ridge; LB, Lau Basin; MAR, Mid-Atlantic Ridge; MCSC, Mid-Cayman Spreading Centre; NFB, North Fiji Basin; OT, Okinawa Trough; SB, Sagami Bay.

Table 2. Morphological variation in *Iheyaspira bathycodon* gen. nov. and sp. nov.

Catalogue no.	Type status	Shell height (mm)	Shell diameter (mm)	No. whorls	Operculum diameter (mm)	Operculum no. rings
11	Holotype	4.3	3.6	4.3	1.8	11
01	Paratype	6.7	5.9	4.5	1.8	11
02**	Paratype	5.2	4.3	4.5	2.1	13
03	Paratype	5.4	5.1	4.2	1.8	14
04	Paratype	5.9	5.5	4.3	2.2	17
05	Paratype	4.8	4.2	4.3	2.3	12
06	Paratype	3.7	3.62	3.55	1.4	9
07*	Paratype	6.9	5.64	4.6	3.3	16
08**	Paratype	6.7	6.5	4.6	2.6	13
09	Paratype	6.4	5.0	4.65	2.5	14
10	Paratype	7.2	6.1	4.4	2.8	14

*soft parts dissected out of shell; ** soft parts dissected out of shell and used for scanning electron microscopy.

Please note that the type material will be deposited at NHMUK after reviewers' comments have been received; the catalogue numbers will be inserted into the table and manuscript immediately.