



## On the systematics and ecology of two new species of *Provanna* (Gastropoda: Provannidae) from deep-sea hydrothermal vents in the Caribbean Sea and Southern Ocean

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### ABSTRACT

The recent discovery and exploration of deep-sea hydrothermal vent fields in the Mid-Cayman Spreading Centre, Caribbean Sea (Beebe Vent Field, 4956–4972 m depth) and the East Scotia Ridge, Southern Ocean (E2 and E9 vent fields, 2394–2641 m depth) have yielded extensive collections of two new provannid species, *Provanna beebei* n. sp. and *P. cooki* n. sp. Morphological and molecular taxonomy (530 bp of the mitochondrial cytochrome *c* oxidase subunit I gene) confirm *P. beebei* n. sp. and *P. cooki* n. sp. as distinct species; these species are formally described, and details are provided of their distribution, habitat and species associations. Bayesian and maximum likelihood analyses support the placement of *P. beebei* n. sp. and *P. cooki* n. sp. within the genus *Provanna* and show that these two new deep-sea species form a well-supported clade with the abyssal West Pacific *P. cingulata*. *Provanna beebei* n. sp. and *P. cooki* n. sp. represent the first records of *Provanna* from hydrothermal vents in the Caribbean Sea and Southern Ocean, respectively, and extend the known geographic range of the genus. For the first time, intraspecific phenotypic variation in size and sculpture has been reported for *Provanna*. At the East Scotia Ridge, shell-size frequency distributions and median shell size of *P. cooki* n. sp. varied significantly between the E2 and E9 vent fields, as well as between diffuse flow and high-temperature venting habitats within each field. The variation in shell sculpture in relation to habitat was also observed in *P. cooki* n. sp.

### INTRODUCTION

Hydrothermal vent environments have become important models for understanding the origins and limits of life (e.g. Martin *et al.*, 2008; Takai, 2011; Clarke, 2014) and for investigating the evolution of island-like communities in the deep sea (Rogers *et al.*, 2012). In addition, these environments are considered to be a potential source of natural products (Thornburg *et al.*, 2010) and mineral resources (Boschen *et al.*, 2013). Vent habitats and their associated endemic species assemblages are patchy in distribution and transient in persistence (Collins *et al.*, 2013). These habitats are linearly spread along oceanic ridges or haphazardly distributed across back-arc basins, at low to high latitudes (Beaulieu *et al.*, 2013).

Since the discovery of hydrothermal vents along the Galapagos Rift in 1977, gastropods have become recognized as a major component of the chemosynthesis-based faunal assemblages of vent fields in the back-arc basins of the western Pacific and mid-ocean ridges including the Central- and Southwest-Indian Ridges, the Mid-Atlantic Ridge and the Mid-Cayman Spreading Centre (Nakamura *et al.*, 2012; Nye *et al.*, 2013a and references therein; Wheeler *et al.*, 2013). Gastropods are one of the most species-rich macrofaunal taxa from hydrothermal vents and

hydrocarbon seeps (Warén, Bouchet & von Cosel, 2006). This molluscan fauna includes large species, such as *Alviniconcha* spp. (Okutani & Ohta, 1988; Johnson *et al.*, 2015) and *Ifremeria nautilei*, as well as morphologically unusual ones like the scaly-foot gastropod (Warén *et al.*, 2003; Chen *et al.*, 2015) *Chrysomallon squamiferum*. Interest in gastropods of deep-sea chemosynthetic environments has also been heightened by observations of the diverse symbiotic relationships between vent molluscs and bacteria (e.g. Borowski *et al.*, 2002; Suzuki *et al.*, 2006; Bates, 2007). Most other gastropod species associated with vents, seeps and organic falls (animal carcasses, wood) graze on bacterial mats or whale bones, or feed on suspended food particles (Johnson *et al.*, 2010).

The superfamily Abysochrysoidea Tomlin, 1927, as currently understood (Sasaki *et al.*, 2010), includes the extant families Abysochrysidae Tomlin, 1927 and Provannidae Warén & Ponder, 1991. Johnson *et al.*'s (2010) multigene, molecular phylogenetic study of the Abysochrysoidea suggested that the Provannidae is paraphyletic. This family, which is known from vents, seeps and organic falls in the deep ocean (Amano & Little, 2014), includes the extant genera *Provanna* Dall 1918; *Alviniconcha* Okutani & Ohta, 1988; *Cordesia* Warén & Bouchet, 2009; *Desbruyeresia* Warén &

Bouchet, 1993; and *Ifremeria* Bouchet & Warén, 1991 (Reynolds *et al.*, 2010; Sasaki *et al.*, 2010). *Provanna* is the most species-rich of these genera. It is currently represented by 21 described species, which together occur across a bathymetric range of 450–5687 m (Table 1), and includes seven formally described fossil species (Amano & Little, 2014). Most *Provanna* species graze on filamentous bacteria, although some are deposit feeders (Sasaki *et al.*, 2010). Bergquist *et al.* (2007) suggested that *Provanna variabilis* Warén & Bouchet, 1986 may host symbiotic bacteria, but this is doubtful given the anatomy of this species (Sasaki *et al.*, 2010).

During recent deep-sea expeditions of newly discovered hydrothermal vent fields on the Mid-Cayman Spreading Centre (RV 'Atlantis' voyage 18-16 and RSS James Cook voyage JC82; Connelly *et al.*, 2012) and the East Scotia Ridge (RSS James Cook voyage JC42; Rogers *et al.*, 2012), provannid gastropods of different morphotypes and sizes were observed (Fig. 1). These were extensively sampled for subsequent taxonomic and ecological analyses. Species from chemosynthetic habitats like vents and seeps are often endemic to the locality in which they are found. Newly discovered sites, therefore, often lead to descriptions of new taxa. Vrijenhoek (2009) recognized the difficulty of identifying chemosynthetic fauna on the basis of insufficient morphological and molecular systematic data and emphasized that, in estimating species diversity, cryptic species and species with high phenotypic plasticity are a source of substantial uncertainty. Due to inadequate sampling of chemosynthetic sites characterized by fine-scale heterogeneity in physical and chemical parameters (Luther *et al.*, 2001), only a subset of the intraspecific morphological variability at a site may be sampled. Moreover, size- or sex-based habitat partitioning in species micro-distributions may not be detected (Bates, 2008). In comparison with intertidal or terrestrial species, ecological data on deep-sea species are scarce (e.g. Wilding, Butlin & Grahame, 2001; Irie, 2006; Nakano & Spencer, 2007; Charrier *et al.*, 2013), and far less is known about the relative importance of local adaptation *vs* ecophenotypic variation in shaping the morphological diversity observed in deep-sea habitats.

The aims of this paper are: (1) to describe two new species of *Provanna* from vent sites in the Caribbean Sea and the Southern Ocean and compare their morphology with the other species of *Provanna* described to date; (2) using DNA sequence data for the mitochondrial cytochrome *c* oxidase subunit I (COI) gene, to determine if the new species are genetically distinct from each other and all other provannid species in the GenBank database; (3) to determine, as far as possible, if there is significant variation in the shell-size frequency distributions of the sampled populations of the new species, within and between vent fields; and (4) to assess spatial variation in morphology among populations of vent-endemic species.

## MATERIAL AND METHODS

### Sample collection

Specimens were collected from the Beebe Vent Field (depth range: 4956–4972 m) at the Mid-Cayman Spreading Centre, Caribbean Sea (Connelly *et al.*, 2012) and the E2 and E9 vent fields (400 km apart; depth range: 2394–2641 m) on the East Scotia Ridge, Southern Ocean (Rogers *et al.*, 2012). Sampling was done using the suction samplers of two remotely operated vehicles (ROVs), 'Jason-II' and 'Isis' (Fig. 1). Detailed site descriptions and maps for the Beebe Vent Field were given by Connelly *et al.* (2012) and for the E2 and E9 fields by Rogers *et al.* (2012). During both expeditions, all provannid specimens were preserved in 96% precooled ethanol; 96% ethanol was also used for permanent preservation. Note that this preservation medium often makes tissue brittle.

### Morphology

Shell length and width were measured to the nearest 0.1 mm using digital Vernier callipers. Scanning electron microscopy (SEM) of shells (uncoated), opercula (uncoated) and radulae (gold coated) was performed using a Hitachi TM3000 SEM machine at the British Antarctic Survey (BAS). Shells and associated opercula were placed in an ultrasonic cleaning bath for 3 min. Radulae were prepared by dissecting the radula sacs and dissolving them in 25% potassium hydroxide to expose the radulae. The radulae were then cleaned using fine brushes and placed on carbonate sticker SEM stubs.

### Molecular systematics

Genomic DNA was successfully extracted from *Provanna* from the Beebe field with the DNeasy Blood & Tissue Kit (Qiagen, Crawley, West Sussex, UK), as directed by the manufacturer. PCR amplifications of the COI region were performed using high-fidelity velocity polymerase (Bioline, London, UK) in 15-ml reactions with 0.2 mM LCO and HCO variant primers (Goddall-Copestake, 2014). We used *c.* 3 ng of template and a thermocycling profile of 50 s at 98 °C, 35 cycles × (10 s at 98 °C, 10 s at 56 °C), ending with 90 s at 72 °C. Sequencing was performed at Source Biosciences, Cambridge, UK.

For *Provanna* from E2 and E9 fields on the East Scotia Ridge, genomic DNA was extracted using the DNeasy Blood & Tissue Kit, and the COI region was amplified with the primer pair LCO1490 and HCO2198 (Folmer *et al.*, 1994). PCR amplification was carried out in 20 µl reactions and included 1 µl each of primer mix at 10 µM and 15–30 ng of template (15–30 ng/µl). The PCR protocol consisted of the following steps: 1 min at 95 °C; 35 cycles × (15 s at 95 °C, 15 s at 40 °C, 30 s at 72 °C); and a final step of 7 min at 72 °C. Successful PCR products were purified using ExoSAP-IT (Affymetrix), following standard protocols. Cycle sequencing reactions were carried out as follows: 1 min at 96 °C; 25 cycles × (10 s at 96 °C, 5 s at 50 °C, 75 s at 60 °C); and a final step of 4 min at 60 °C. Sequencing was done using an Applied Biosystems 3130xl DNA sequencer (JAMSTEC). The GenBank accession numbers for the newly generated partial COI sequences are MK790057–MK790067.

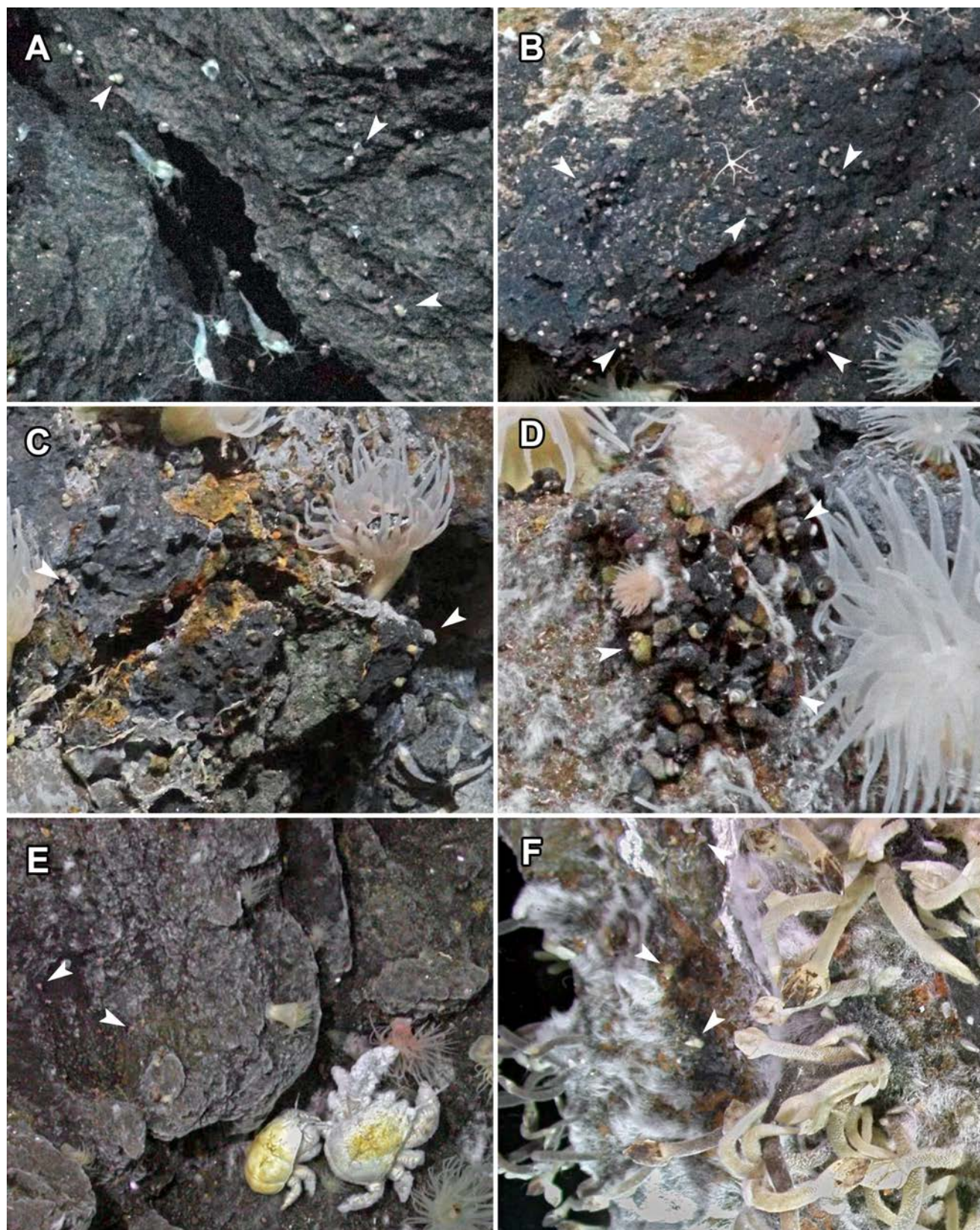
Using Geneious v. 5.6 (Drummond *et al.*, 2011), complementary sequences from the forward and reverse primers were aligned to assess sequencing accuracy. Phylogenetic analyses were carried out using MEGA 6 (Tamura *et al.*, 2013); the dataset comprised the sequence data generated by us and abyssochrysid COI sequences obtained from GenBank. Following Johnson *et al.* (2010) and Chen *et al.* (2018), the outgroup included the whelks *Neptunea amianta* (Dall, 1890) and *N. antiqua* (Linnaeus, 1758) and the periwinkle *Littorina littorea* (Linnaeus, 1758).

Bayesian analysis was conducted using MrBayes v. 3.2 (Ronquist *et al.*, 2012). The nucleotide substitution models used were GTR + I + G for the first and second codons and HKY + G for the third codon; these models were selected using the Bayesian information criterion in PartitionFinder v. 1.0.1 (Lanfear *et al.*, 2012). MCMC chains were run for 5 million generations, topologies were sampled every 100 generations and the first 25% of trees were discarded as 'burn-in'. Convergence was checked using Tracer v. 1.6 (Rambaut, Suchard & Drummond, 2013) to determine the adequate 'burn-in' values. The maximum likelihood (ML) tree was generated with MEGA; we used 2000 bootstrap replicates and the GTR + I + G model (selected as the most suitable substitution model by the model selection programme within MEGA).

### Deposition of type material

The holotypes are deposited in the invertebrate collection at the Natural History Museum, London (NHM, registration numbers have the prefix NHMUK), UK. Paratypes as well as other specimens used in the morphometric analysis are deposited in the NHM,





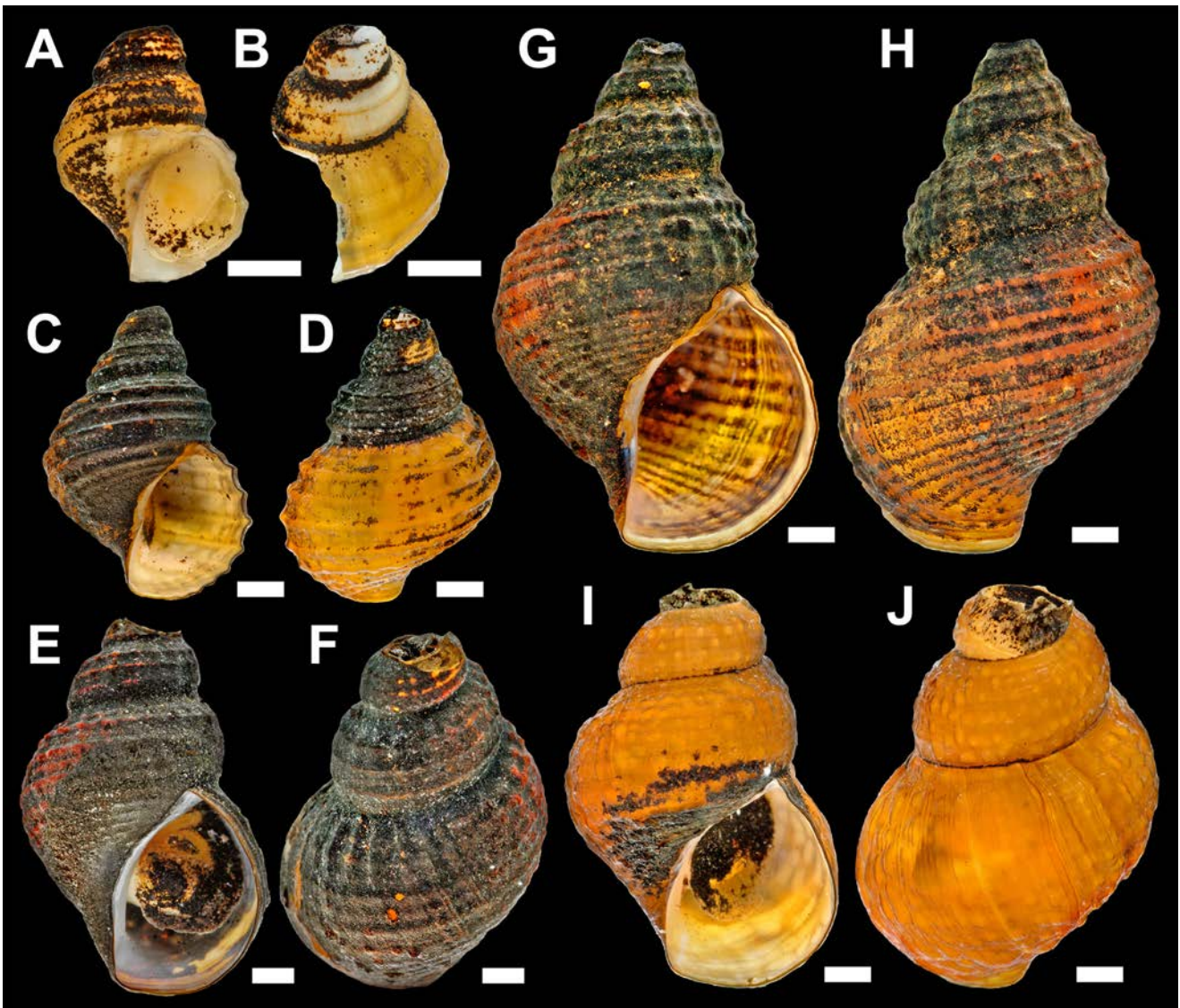
**Figure 1.** *Provanna beebi* n. sp. (A–D) and *P. cooki* n. sp. (E, F) in their natural habitat (the snails are indicated by white arrows). **A.** With the shrimp *Rimicaris hybisae* (Beebe Chimlets). **B.** With the ophiuroid *Ophiactinella acies* and actinostolid anemones (Beebe Chimlets). **C.** With *R. hybisae* and actinostolid anemones (Anemone Field). **D.** With microbial mat and actinostolid anemones (Beebe Chimlets). **E.** With yeti crab *Kiwa tyleri* and actinostolid anemones (E2 Dog's Head). **F.** With stalked barnacles *Neolepas scotiaensis*, amphipods and microbial mat (E9 Marsh Tower). Images taken using the ROV 'Isis'.



**Table 1.** Provanniid gastropods described from the deep sea. Only formally described species and confirmed localities are given.

Species	Locality	Depth (m)	Habitat type			Primary references
			Vent	Seep	Organic falls	
<i>Provanna abyssalis</i> Okutani & Fujikura, 2002	West Pacific: Japan Trench	5379		x		Okutani & Fujikura (2002); Sasaki, Okutani & Fujikura (2005)
<i>P. admetoides</i> Warén & Ponder, 1991	West Atlantic: Florida Escarpment	624–631		x		Warén & Ponder (1991); Warén & Bouchet (1993)
<i>P. beebel</i> sp. nov.	Caribbean: MCSC Beebe Vent Field	4956–4972	x			<b>This study</b>
<i>P. buccinoides</i> Warén & Bouchet, 1993	West Pacific: Lau & North Fiji basins	1900–2765	x			Warén & Bouchet (1993); Warén & Bouchet (2001); Warén <i>et al.</i> in Desbruyères <i>et al.</i> (2006)
<i>P. chevallieri</i> Warén & Bouchet, 2009	East Atlantic: Regab Site	3150		x		Warén & Bouchet (2009)
<i>P. cingulata</i> Chen, Watanabe & Ohara, 2018	West Pacific: Shinkai Seep Field	5687		x		Chen <i>et al.</i> (2015)
<i>P. clathrata</i> Sasaki, Ogura, Watanabe & Fujikura, 2016	West Pacific: Okinawa Trough	1647–2165	x			Sasaki <i>et al.</i> (2016); Miyazaki <i>et al.</i> (2017)
<i>P. cooki</i> sp. nov.	Southern Ocean: ESR E2 & E9	2394–2641	x			<b>This study</b>
<i>P. fenestrata</i> Chen, Watanabe & Sasaki, 2019	West Pacific: Okinawa Trough	1559–1973	x			Chen <i>et al.</i> (2019)
<i>P. glabra</i> Okutani, Tsuchida & Fujikura, 1992	West Pacific: Sagami Bay	1110–1200		x		Okutani, Tsuchida & Fujikura (1992); Warén & Bouchet (2001); Warén <i>et al.</i> in Desbruyères <i>et al.</i> (2006)
<i>P. goniata</i> Warén & Bouchet, 1986	East Pacific: Guaymas Basin	2000–2020		x		Warén & Bouchet (1986); Warén & Ponder (1991); Warén & Bouchet (2001)
<i>P. ios</i> Warén & Bouchet, 1986	East Pacific: EPR (21°N, 17°S), GSC	2450–2620	x			Warén & Bouchet (1986); Warén & Ponder (1991); Warén & Bouchet (2001); Warén <i>et al.</i> in Desbruyères <i>et al.</i> (2006)
<i>P. kuroshimensis</i> Sasaki, Ogura, Watanabe & Fujikura, 2016	West Pacific: Okinawa Trough	644		x		Sasaki <i>et al.</i> (2016)
<i>P. laevis</i> Warén & Ponder, 1991	East Pacific: Gulf of California; Guaymas Basin to Oregon Margin, JdFR	500–2000	x	x		Warén & Ponder (1991); Warén & Bouchet (2001); Warén <i>et al.</i> in Desbruyères <i>et al.</i> (2006)
<i>P. lonana</i> (Dall, 1918)	East Pacific: Oregon Margin	450–1200		x		Dall (1918); Warén & Bouchet (1986); Warén & Bouchet (2001)
<i>P. lucida</i> Sasaki, Ogura, Watanabe & Fujikura, 2016	West Pacific: Okinawa Trough	701	x			Sasaki <i>et al.</i> (2016)
<i>P. macleani</i> Warén & Bouchet, 1989	East Pacific: Oregon Margin	2713–2750		x	x	Warén & Bouchet (1989); Warén & Bouchet (2001)
<i>P. muricata</i> Warén & Bouchet, 1986	West Pacific: GSC	2450–2615	x			Warén & Bouchet (1986); Warén & Ponder (1991)
<i>P. nassariaeformis</i> Okutani, 1990	West Pacific: Mariana Back-Arc Basin	3670–3680	x			Okutani (1990); Warén & Bouchet (2001); Warén <i>et al.</i> in Desbruyères <i>et al.</i> (2006)
<i>P. pacifica</i> (Dall, 1908)	Gulf of Panama	2311				Dall (1908); Warén & Bouchet, (1986)
<i>P. reticulata</i> Warén & Bouchet, 2009	East Atlantic: Regab, Guinness & MPS-1 Congo sites	750–3150		x		Warén & Bouchet (2009)
<i>P. sculpta</i> Warén & Ponder, 1991	GoM: Louisiana Slope	550		x		Warén & Ponder (1991); Warén & Bouchet (2001)
<i>P. segonzaci</i> Warén & Ponder, 1991	West Pacific: Lau Back-Arc Basin	1750–1900	x			Warén & Ponder (1991); Warén & Bouchet (1993); Warén & Bouchet (2001); Warén <i>et al.</i> in Desbruyères <i>et al.</i> (2006)
<i>P. shinkaiae</i> Okutani & Fujikura, 2002	West Pacific: Japan Trench	5343		x		Okutani & Fujikura (2002); Sasaki <i>et al.</i> (2005)
<i>P. stephanos</i> Chen, Watanabe & Sasaki, 2019	West Pacific: Sagami Bay	908		x		Chen <i>et al.</i> (2019)
<i>P. subglabra</i> Sasaki, Ogura, Watanabe & Fujikura, 2016	West Pacific: Okinawa Trough	710–2165	x			Sasaki <i>et al.</i> (2016); Miyazaki <i>et al.</i> (2017)
<i>P. variabilis</i> Warén & Bouchet, 1986	East Pacific: JdFR	1519–3232	x	x		Warén & Bouchet (1986); Warén & Ponder (1991); Warén & Bouchet (1993); Gustafson & Lutz (1994); Warén & Bouchet (2001); Kiel (2004); Warén <i>et al.</i> in Desbruyères <i>et al.</i> (2006)

Abbreviations are: EPR, East Pacific Rise; ESR, East Scotia Ridge; GoM, Gulf of Mexico; GSC, Galapagos Spreading Centre; JdFR, Juan de Fuca Ridge; MCSC, Mid-Cayman Spreading Centre.



**Figure 2.** *Provanna beebel* n. sp., Beebe Vent Field. **A, B.** Paratype 1 (NHMUK 20190544). **C, D.** Paratype 2 (NHMUK 20190545). **E, F.** Paratype 3 (NHMUK 20190546). **G, H.** Holotype (NHMUK 20190543). **I, J.** Paratype 4 (NHMUK 20190547). Scale bar = 1 mm.

the Cambridge Zoology Museum, Cambridge, UK (UMZC), the Museum National d'Histoire Naturelle (MNHN), Paris, France and the University Museum, University of Tokyo (UMUT), Japan.

## SYSTEMATIC DESCRIPTIONS

### Superfamily ABYSSOCHRYSOIDEA Tomlin, 1927

### Family PROVANNIDAE Warén & Ponder, 1991

### Genus *Provanna* Dall, 1918

### *Provanna beebel* new species

(Figs 1–3)

*Provanna* sp. Plouviez *et al.*, 2015: table 1, fig. 2E.

**Type material:** Holotype: Beebe Chimlets, Beebe Vent Field, Mid-Cayman Spreading Centre, 18°32.799'N, 81°43.139'W, 4972 m (11 January 2014, ROV 'Jason-2', RV 'Atlantis' voyage 18-16); NHMUK 20190543 (Fig. 2G, H). Paratypes 1–3: same locality as holotype; paratype 1: NHMUK 20190544 (Fig. 2A, B); paratype 2: NHMUK 20190545 (Fig. 2C, D); paratype 3: NHMUK 20190546

(Fig. 2E, F). Paratypes 4–6: Anemone Field, Beebe Vent Field, Mid-Cayman Spreading Centre, 18°32.815'N, 81°43.101'W, 4956 m (24 February 2014, ROV 'Isis', RRS 'James Cook' voyage JC82); paratype 4: NHMUK 20190547 (Fig. 2I, J); paratype 5: NHMUK 20190548 (Fig. 3A, B); paratype 6: NHMUK 20190549 (Fig. 3C). Paratypes 5 and 6 are dissected and mounted for SEM imaging.

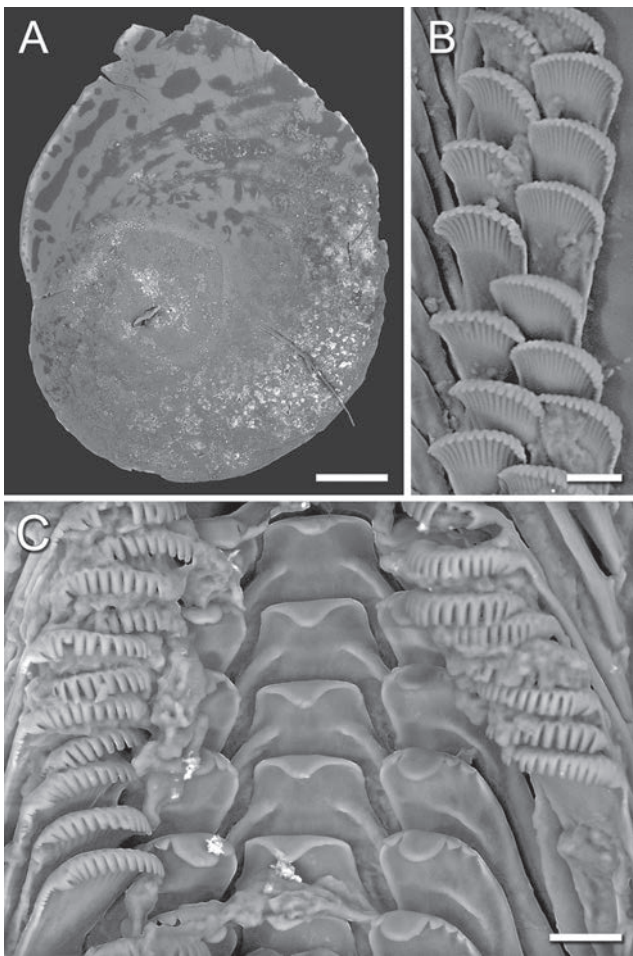
**Other material examined:** A total of 103 specimens from same lot as holotype and paratypes 1–3 (NHMUK 20190550). A total of 45 specimens from same lot as paratypes 4–6 (NHMUK 20190551); DNA was extracted from 2 of these specimens.

**Etymology:** Named after the type locality, the Beebe Vent Field.

**ZooBank registration:** urn:lsid:zoobank.org:act:92F95A7B-3BD0-4DF2-964D-CCB87CB80D20.

**Description:** Shell (Fig. 2) sturdy, length greater than width; maximum dimensions: 12.7 mm long, 8.8 mm wide. Surface and apical region corroded in all specimens; protoconch and whorls of early teleoconch lost. Metallic, golden shell periostracum covered by black encrustation of varying thickness and coverage. Shell surface cancellated in appearance due to strong spiral and axial sculpture.





**Figure 3.** *Provanna beebei* n. sp., SEM images. **A.** Operculum (paratype 5, NHMUK 20190548). **B.** Radula (paratype 5, NHMUK 20190548). **C.** Lateral teeth of radula (paratype 6, NHMUK 20190549). Scale bar: **A** = 1 mm; **B, C** = 50 µm.

Penultimate whorls and body whorl have 3 or 4 prominent spiral ribs and irregular secondary ribs; spiral ribs crossed by weakly defined axial ribs with granules at intersections. Base of body whorl weakly inflated, bearing 4 to 9 strong spiral ribs that become less conspicuous and smooth towards the abapical end. Umbilicus absent. Aperture pyriform. No nacre or lustre on internal wall or on shell exterior. Outer lip thin, crenulated; crenulations correspond to extremities of spiral ribs and grooves between ribs and less pronounced in more corroded specimens, giving smoother appearance to outer lip. Inner lip curved slightly, continuous with columellar lip; columellar lip weakly twisted, with shallow sinus. Operculum (Fig. 3A) deeply retracted *in situ*, smaller than aperture, transparent, paucispiral, oval in outline; length 3.3 mm, width 2.5 mm (in a specimen of 9.1 mm shell length, 7.3 mm width, with 2 whorls remaining and corroded apex; from same lot as paratypes 5 and 6).

Radula (Fig. 3B, C) taenioglossate, bilaterally symmetrical, formula 2-1-1-1-2; length 1.4–3.5 mm, width 0.2–2.1 mm, with 78–120 transverse rows. Central tooth differentiated in form from lateral tooth; low trapezoid shape, wider proximally than distally, with elongated and pointed basal edges, single incurved triangular blunt cusp. Lateral tooth of similar size to central tooth, elongate oval shape, incurved inner edge with large, round central cusp flanked on both sides by 2 or 3 smaller blunt cusps that decrease in size towards lateral margins of radula. Inner and outer marginal teeth (Fig. 3C) similar in size, mushroom shaped with elongated

stalk, broadened recurved rake-like top, bearing 13–17 comb-like cusps with several flanking serrations. Soft parts opaque white after preservation; no visible eye.

**Distribution and habitat:** This species is known only from the type locality, the Beebe Vent Field Caribbean Sea at a depth of 4956–4972 m. Mean population density, 263 (SD = 67) individuals/m<sup>2</sup> (based on an analysis of eight images; area estimated using lasers placed a known distance apart). Connelly *et al.* (2012) have given an overview of the geological, geochemical and biological setting of the Beebe Vent Field. The species was observed at and sampled from the Anemone Field area (Fig. 1C, D) on the upper slopes of the west mound of the Beebe Vent Field, at temperatures of 4.07–4.75 °C. It was found in close proximity to diffuse hydrothermal flow from fissures, on black rock with mats of filamentous microbes, actinostolid anemones and the alvinocaridid shrimp *Rimicaris hybisae* (Fig. 1C, D). *Provanna beebei* n. sp. has also been sampled at the Beebe Chimneys (Fig. 1A, B) on the northeast slope of the west mound of the Beebe Vent Field. Here, it was found with *R. hybisae* and the ophiuroid *Ophioclinella acies*, on black rock near small microchimneys and diffuse flow sources.

**Remarks:** *Provanna beebei* n. sp. superficially resembles *P. chevalieri* Warén & Bouchet, 2009 and *P. macleani* Warén & Bouchet, 1989. The new species is readily distinguished from *P. chevalieri* by the absence of a siphonal canal and matt (vs shiny) periostracum. *Provanna beebei* n. sp. exhibits spiral and axial shell sculpture, whereas in *P. macleani* the sculpture is primarily spiral. The latter species also has a radula with a thin, reduced central tooth lacking basal supports. *Provanna beebei* n. sp. differs from the recently described *P. cingulata* Chen, Watanabe & Ohara, 2018 and from *P. cooki* n. sp. in having both spiral and axial sculpture; both *P. cingulata* and *P. cooki* have spiral ribs only. The new species is geographically closest to *P. admetoides* (Florida Escarpment) and *P. sculpta* (Louisiana Slope) from cold seeps, but differs markedly in sculpture. The occurrence of *P. beebei* at the Beebe Vent Field extends the known geographic range of *Provanna* into the Caribbean (see Table 1).

### *Provanna cooki* new species

(Figs 1, 4–6)

Provannid gastropod Rogers *et al.*, 2012: 7, 9.

Provannid sp. 1 Rogers *et al.*, 2012: table 2.

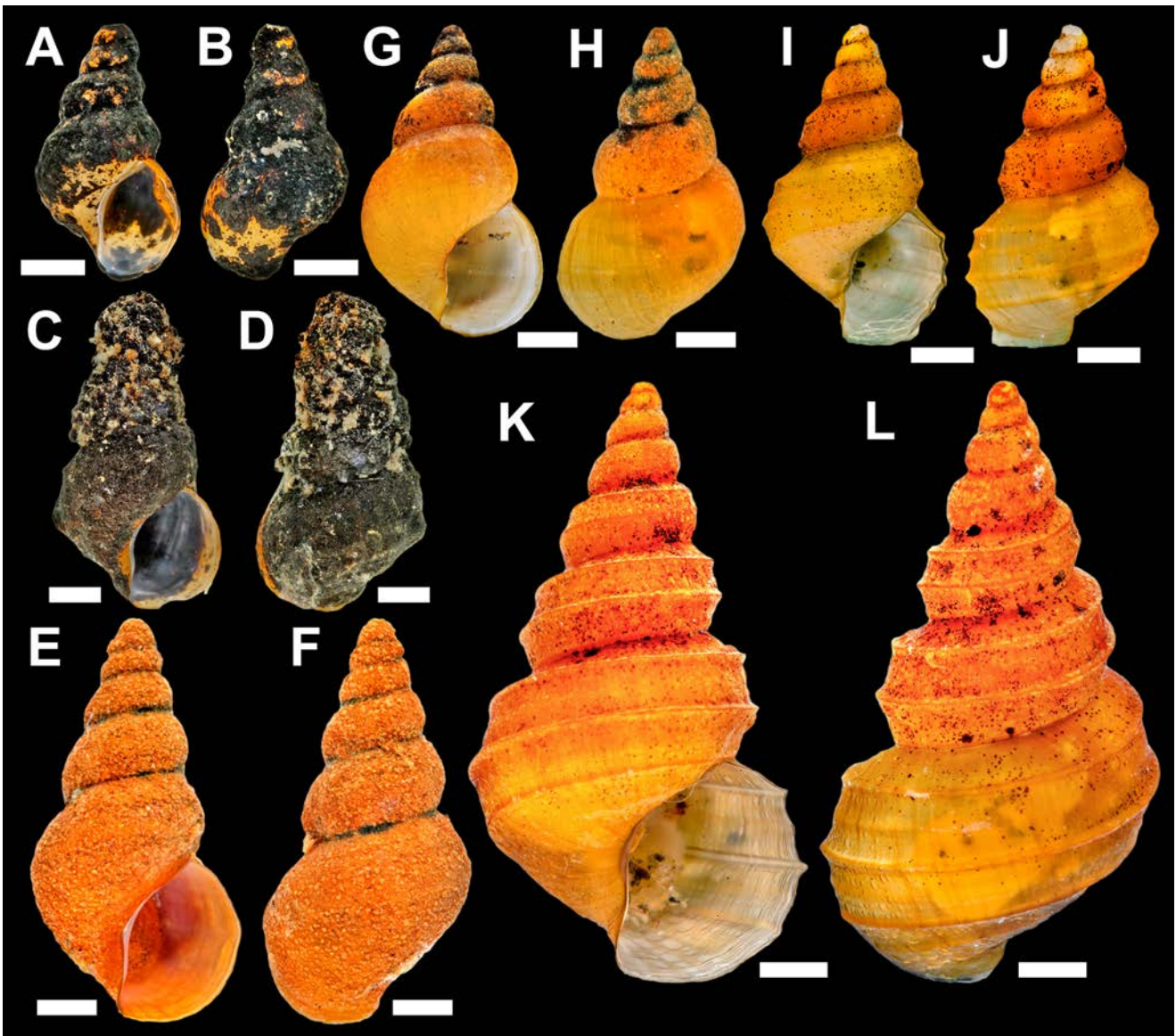
Provannid sp. 2 Rogers *et al.*, 2012: table 2.

Provannidae sp. 1 and sp. 2 Reid *et al.*, 2013: 3, 8, table 3.

Provannidae sp. 1 and sp. 2 Rogers & Linse, 2014: 243, table 1.

**Type material:** Holotype: SW Field, East Scotia Ridge segment E9, 60°02.823'S, 29°58.696'W, 2396 m (2 February 2010, ROV 'Isis', RRS 'James Cook' voyage JC42); NHMUK 20190552 (Fig. 4K, L); shell length 7.2 mm, width of ultimate whorl 4 mm (7 whorls in total, with 3 distinct spiral ribs).

Paratypes 1, 2: Anemone Field, East Scotia Ridge segment E2, 56°05.277'S, 30°19.087'W, 2603 m (24 January 2010, ROV 'Isis', RRS 'James Cook' voyage JC42); paratype 1: MNHN-IM-2000-34 740 (Fig. 4A, B); paratype 2: UMZC 2019.5 (Fig. 4C, D). Paratype 3: diffuse flow under the Dog's Head chimney, East Scotia Ridge segment E2, 56°05.335'S, 30°19.100'W, 2627 m (23 January 2010, ROV 'Isis', RRS 'James Cook' voyage JC42); UMZC 2019.6 (Fig. 4E, F). Paratype 4: Anemone Field, East Scotia Ridge segment E2, 56°05.277'S, 30°19.087'W, 2603 m (24 January 2010, ROV 'Isis', RRS 'James Cook' voyage JC42); UMUT RM33144 (Fig. 4G, H). Paratype 5: Marsh Tower, East Scotia Ridge segment E9, 60°02.807'S, 29°58.708'W, 2605 m (2 February 2010, ROV 'Isis', RRS 'James Cook' voyage JC42); MNHN-IM-2000-34741 (Fig. 4I, J). Paratype 6: Dog's Head, East Scotia Ridge segment E2, 56°05.313'S, 30°19.087'W, 2605 m (20 January 2010, ROV 'Isis', RRS 'James Cook' voyage JC42);



**Figure 4.** *Provanna cooki* n. sp. **A, B.** Paratype 1 (MNHN-IM-2000-34 740). **C, D.** Paratype 2 (UMZC 2019.5). **E, F.** Paratype 3 (UMZC 2019.6). **G, H.** Paratype 4 (UMUT RM33144). **I, J.** Paratype 5 (MNHN-IM-2000-34 741). **K, L.** Holotype (NHMUK 20190552), SW Field. Scale bar = 1 mm.

NHMUK 20190553 (Fig 5A–C). Paratype 7: Deep Castle, East Scotia Ridge segment E2, 56°05.325'S, 30°19.057'W, 2639 m (24 January 2010, ROV 'Isis', RRS 'James Cook' voyage JC42); NHMUK 20190554 (Fig 5D, E). All type specimens are in an intact state apart from paratypes 6 and 7, which were dissected for SEM imaging.

**Other material examined:** A total of 107 specimens from same lot as the holotype (NHMUK 20190555), of which 3 specimens extracted for DNA. A total of 146 specimens from the same lot as paratypes 1, 2 and 4 (MNHN-IM-2000-34 742), of which 3 specimens extracted for DNA. Twenty specimens from the same lot as paratype 3 (UMZC 2019.7), of which 3 specimens extracted for DNA. Twenty two specimens from the same lot as paratype 5 (MZC 2019.8). One egg case from the same lot as paratype 5 (NHMUK 20190556). One specimen from the same lot as paratype 6 (NHMUK 20190557). Thirteen specimens from the same lot as paratype 7 (UMUT Mo-RM33145).

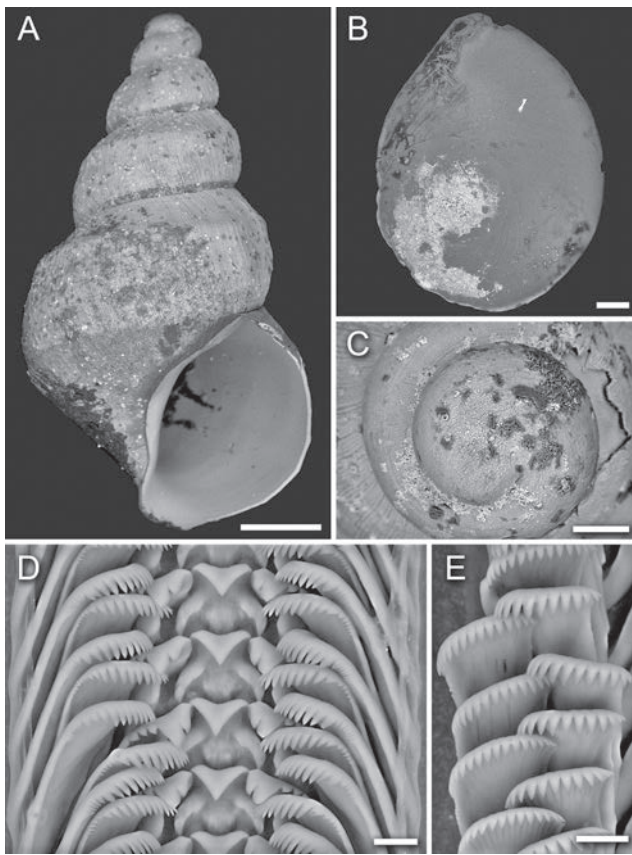
**Etymology:** Named after Captain James Cook, who discovered the South Sandwich Islands during his second voyage in 1775. The new

species was sampled by the research ship RRS 'James Cook' on its first voyage to the Southern Ocean.

**ZooBank registration:** urn:lsid:zoobank.org:act:9C808A95-4F19-4AC9-8B05-E45E8DDCF237.

**Description:** Shell (Figs 4, 5A) rather high, slender, turreted, length greater than width; maximum dimensions: 15.0 mm long, 8.2 mm wide. Metallic, golden shell periostracum, covered by rust-coloured or black encrustation. Shell surface and apical region corroded or covered in crust to varying degree, with protoconch and whorls of early teleoconch missing in some specimens. Protoconch *c.* 1.5 whorls; no clear boundary visible between prodissococonch I and teleoconch (Fig 5C). Protoconch II absent, indicating direct development in this species. Sculpture of protoconch initially finely granulate, later increasingly consisting of fine spiral lines. Diameter of teleoconch at first whorl *c.* 240 µm, at 1.5 whorls *c.* 300 µm. Shell sculpture variable, with two morphotypes, one relatively smooth (Figs 4A–H, 5A), the other with well defined spiral sculpture (Fig 4I–L). In spirally ribbed specimens, penultimate whorls and body whorl have 2 to 4 spiral ribs that are crossed by weakly

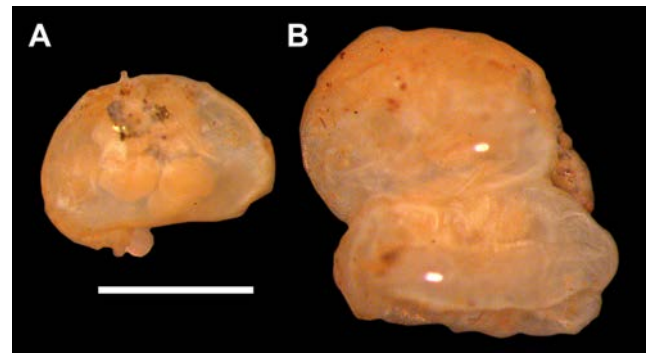




**Figure 5.** *Provanna cooki* n. sp., SEM images. **A.** Shell (paratype 6, NHMUK 20190553); 3.2 mm long, 1.6 mm wide. **B.** Operculum (paratype 6, NHMUK 20190553). **C.** Apical region of shell (paratype 6, NHMUK 20190553). **D.** Radula (paratype 7, NHMUK 20190554; shell 8.9 mm long, 4.6 mm wide). **E.** Lateral teeth of radula (paratype 7, NHMUK 20190554). Scale bar: **A**, **C** = 1 mm; **B** = 200 µm; **D** = 50 µm; **E** = 25 µm.

defined axial ribs. Base of body whorl weakly inflated, smooth towards abapical end. Umbilicus absent. Aperture oval. Nacre and lustre absent on internal wall and shell exterior. Outer lip thin, crenulated; crenulations correspond to extremities of spiral ribs and grooves between ribs and less pronounced in more corroded specimens so giving outer lip a smooth appearance. Inner lip slightly curved, continuous with columellar lip. Operculum (Fig. 5B) deeply retracted *in situ*, smaller than aperture, transparent, paucispiral with oval outline; length 1.3–3.1 mm, width 1.0–2.3 mm (in specimens of 4–12.4 mm shell length). Radula (Fig. 5D, E) taenioglossate, bilaterally symmetrical, formula 2-1-1-1-2; length 0.8–3.6 mm, width 0.1–0.2 mm, with 23–128 transverse rows (as measured in specimens ranging from 4 to 12.4 mm in shell length). Central tooth differs in shape from lateral teeth; low trapezoid shape, broader proximally than distally, with basal edges elongated and pointed and an incurved triangular pointed cusp. Lateral tooth similar size to central tooth, elongate oval shape, incurved inner edge bearing 5 or 6 pointed cusps, with subcentral cusp most prominent. Inner and outer marginal teeth (Fig. 5E) similar in size, mushroom shaped with elongated stalk, broadened incurved top bearing 13–17 comb-like cusps with several flanking serrations. Preserved soft parts opaque white; not visible eye.

**Distribution and habitat:** This species is known only from the type locality, the hydrothermal vent and diffuse flow fields on the E2 and E9 segments of the East Scotia Ridge, Southern Ocean, at depths ranging from 2394 to 2641 m. The hydrothermal setting of the E2 and E9 segments is characterized by black smoker chimneys



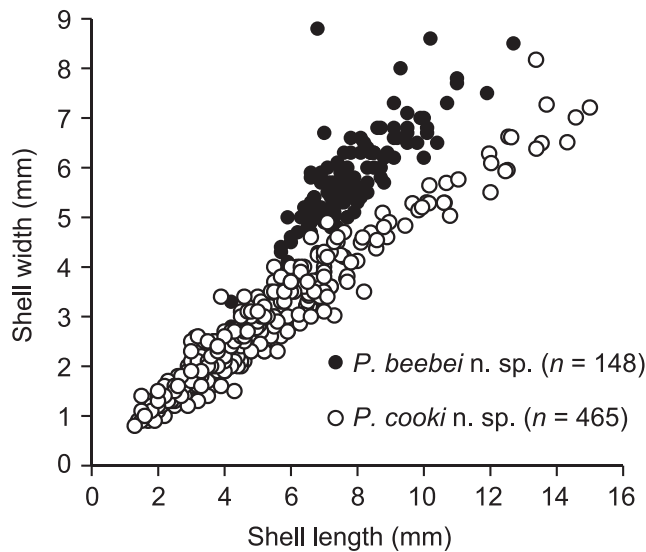
**Figure 6.** Egg capsule of *Provanna cooki* n. sp. (NHMUK 20190556). **A.** Single egg capsule with juveniles visible. **B.** Multiple egg capsules. Scale bar = 1 mm.

and diffuse-flow areas of differing low temperatures. Rogers *et al.* (2012) have provided an overview of the geological, geochemical and biological setting of the E2 and E9 vent fields, and Marsh *et al.* (2012) have described the specific chimney structures and diffuse flow areas within the E9 vent field. These authors have also provided data on the microdistribution of the fauna and defined specific assemblage types on the basis of abiotic (e.g. distance from the vent fluid exit, temperature) and biotic (e.g. presence and dominance of chemosynthetic taxa) factors. At the E2 vent field, the ‘smooth’ morphotype of *P. cooki* n. sp. dominated specimens collected from the sides and bottom of the Dogs’ Head chimneys, where it was found with the yeti crab *Kiwa tyleri* and actinostolid anemones (Fig. 1E). The ‘smooth’ morphotype also dominated collections from the low-venting and peripheral diffuse flow fields at Diffuse (the ‘robust’ morphotype of the stalked barnacle *Neolepas scotiaensis* also occurred here) and the diffuse flow at Deep Castle. Most of the specimens were coated with mineral precipitates that were either black and/or orange in colour.

At the E9 vent field, only the ‘ribbed’ morphotype of *P. cooki* n. sp. was present in collections, and the shells were not covered in mineral precipitates. The gastropods were collected from the ‘barnacle assemblage’ (as defined by Marsh *et al.*, 2012) at Marsh Tower (Fig. 1F) and SW Field. The ‘barnacle assemblage’ is characterized by the ‘gracile’ morphotype of *Neolepas scotiaensis*. At the E9 vent field, the new species was also observed in close proximity to amphipods and microbial mats (Fig. 1F).

**Remarks:** *Provanna cooki* n. sp. lays oval-shaped egg capsules, each of which are approximately  $1.5 \times 1 \times 1$  mm in size and contain 5 or 6 eggs that hatch as juveniles through intracapsular metamorphosis (Fig. 6). The egg capsules can be connected to each other. This observation supports the suggestion by Gustafson & Lutz (1994) that in species of the genus *Provanna* a planktotrophic larval stage does not occur. The sculpture of the protoconch and number of whorls, as reported here for *P. cooki* n. sp., are in agreement with the illustrations of the *Provanna* sp. of Warén & Ponder (1991) and *P. variabilis* of Gustafson & Lutz (1994). The size of the protoconch is considerably smaller in *P. cooki* when compared with *P. cooki* n. sp. (c. 300 µm), *P. variabilis* (c. 390 µm) and *Provanna* sp. (411 µm). The two new species described here are readily distinguished from each other by differences in shell and radula characters; a key difference is the shape of the central and lateral teeth. *P. cooki* n. sp. is morphologically similar to *P. cingulata*. Both species have spiral shell sculpture, but in *P. cooki* there are fewer spiral ribs and wider interspaces between ribs. The two species also differ significantly in radular morphology, with the laterals of *P. cooki* n. sp. bearing only a single inner cusp before the strong central cusp, while the laterals of *P. cingulata* bear 2 or 3 inner cusps. The outer cusps of the lateral teeth of *P. cooki* n. sp. are also much more prominent when compared with *P. cingulata*.





**Figure 7.** Relationship between length and width of shell in *Provanna beebei* n. sp. and *P. cooki* n. sp.

The occurrence of *P. cooki* on the E2 and E9 segments of the East Scotia Ridge represents by far the most southerly record of *Provanna* and thus extends the known geographic range of this genus into the Southern Ocean (see Table 1). The limit of the Antarctic Ocean is defined as 60°S; the Southern Ocean consists of the waters within the Polar Front, and its limits extend northwards beyond 60°S.

## RESULTS

### Shell-size frequency distributions

Shell measurements were taken from 148 specimens of *Provanna beebei* n. sp. and 465 specimens of *P. cooki* n. sp.; of the latter species, 199 specimens (all from E2) belonged to the ‘smooth’ morphotype, and 266 specimens (all from E9) belonged to the ‘ribbed’ morphotype. Shell length correlated positively with shell width in both new species (Spearman correlation: *P. beebei* n. sp.,  $R = 0.80$ ,  $P < 0.0001$ ; *P. cooki* n. sp.,  $R = 0.96$ ,  $P < 0.0001$ ; Fig. 7). Specimens of *P. beebei* n. sp. ranged in shell length from 1.5 to 12.7 mm and in shell width from 1.1 to 8.8 mm (Table 2; Fig. 8). The median shell length of this species was significantly larger at the Anemone Field than the Beebe Chimlets (Mann–Whitney  $U$  test,  $U = 1771.0$ ,  $n_1 = 45$ ,  $n_2 = 103$ ,  $P < 0.01$ ). Specimens of *P. cooki* n. sp. ranged in shell length from 1.3 to 15.0 mm and in shell width from 0.9 to 8.2 mm (Table 2; Fig. 8). Overall, specimens were significantly larger at the E9 Vent Field (median length = 5.7 mm; IQR = 3.5–8.5) than the E2 Vent Field (median length = 4.0 mm; IQR = 3.0–5.0) (Mann–Whitney  $U$  test:  $U = 16578.5$ ;  $n_1 = 266$ ,  $n_2 = 199$ ;  $P < 0.001$ ). There was also significant variation in the shell-size frequency distributions of *P. cooki* n. sp. collected from different locations within the E2 and E9 vent fields (Kruskal–Wallis multisample test:  $H = 78.9$ ;  $df = 4$ ;  $P < 0.001$ ; Fig. 8). At the E2 vent field, median shell length was significantly larger at Diffuse than Deep Castle (Mann–Whitney  $U$  test:  $U = 1091.0$ ;  $n_1 = 20$ ,  $n_2 = 167$ ;  $P < 0.05$ ) and at Dog’s Head than Deep Castle (Mann–Whitney  $U$  test:  $U = 471.5$ ;  $n_1 = 12$ ,  $n_2 = 167$ ;  $P < 0.01$ ). Within the E9 vent field, the median shell length of *P. cooki* n. sp. was significantly larger at Marsh Tower than SW Field (Mann–Whitney  $U$  test:  $U = 3907.5$ ;  $n_1 = 66$ ,  $n_2 = 200$ ;  $P < 0.001$ ).

### Species delimitation analysis

Partial sequences of the COI barcoding region were amplified from two specimens of *P. beebei* n. sp. and nine specimens of *P. cooki* n.

**Table 2.** Variation in shell size (median with inter-quartile range) of *Provanna beebei* n. sp. from the Beebe Vent Field and *P. cooki* n. sp. from the E2 and E9 vent fields.

Species	Location	Shell length (mm)	Shell width (mm)
<i>P. beebei</i> n. sp.	Beebe Chimlets	7.4 (1.5–10.4)	5.5 (1.1–8.8)
<i>P. beebei</i> n. sp.	Anemone Field	7.8 (5.9–12.7)	5.6 (3.2–8.5)
<i>P. cooki</i> n. sp.	E2 Dog’s Head	6.1 (3.3–7.7)	3.1 (1.4–3.8)
<i>P. cooki</i> n. sp.	E2 Deep Castle	3.9 (1.7–8.9)	2.1 (0.9–4.6)
<i>P. cooki</i> n. sp.	E2 Diffuse	4.5 (2.6–7.2)	2.2 (1.5–3.6)
<i>P. cooki</i> n. sp.	E9 Marsh Tower	8.1 (1.4–15.0)	4.3 (0.9–8.2)
<i>P. cooki</i> n. sp.	E9 SW Field	5.0 (1.3–13.2)	3.0 (0.8–6.2)

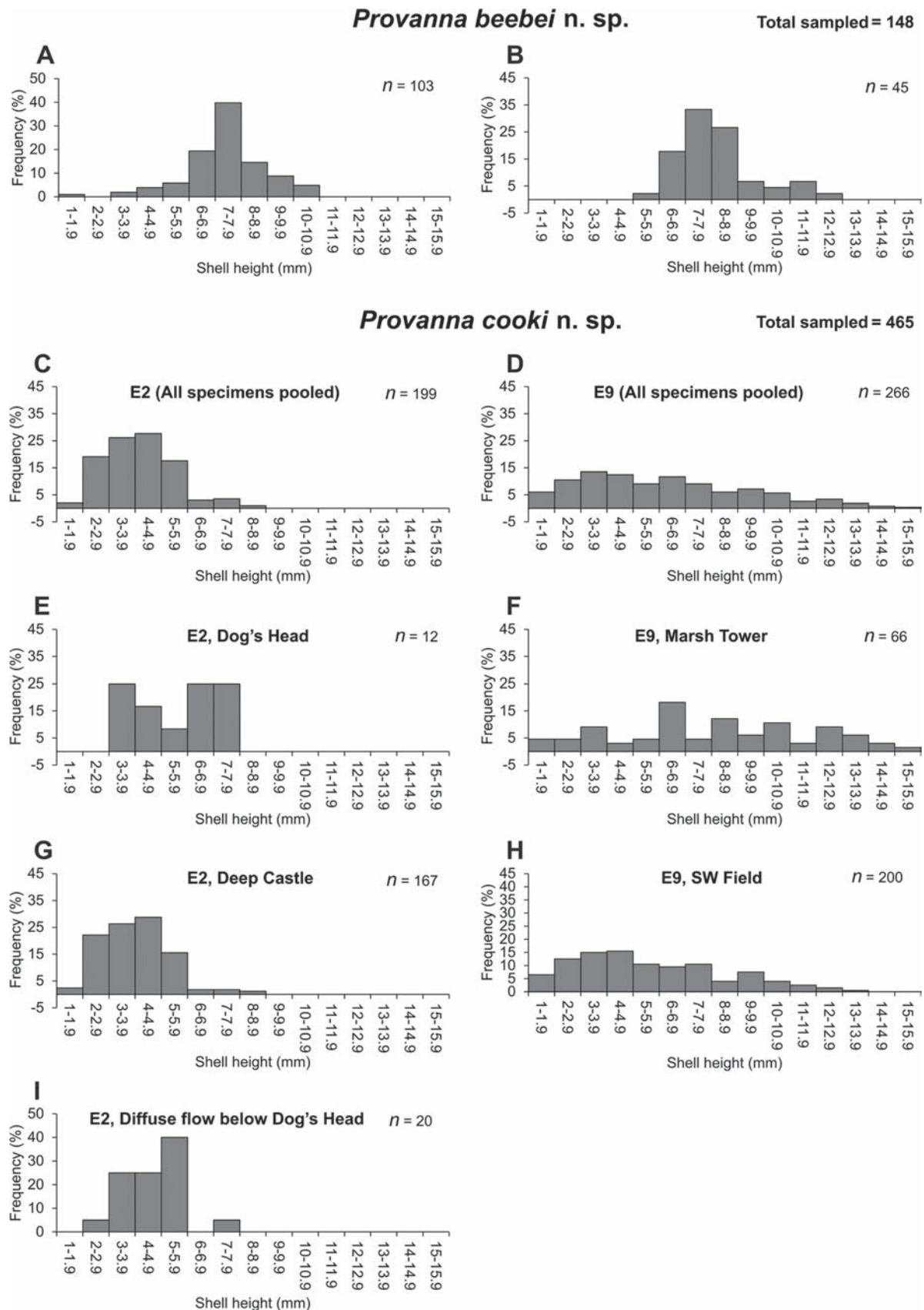
sp. The two new partial COI sequences (623 bp) of *P. beebei* n. sp. were identical to each other, but differed only slightly (uncorrected  $p$ -distance = 1.4%) from the previously published sequence for the *Provanna* sp. SP-2014 (KJ566951) that was collected from the Mid-Cayman Spreading Centre vents by the R/V *Atlantis* expedition AT18–16 (Plouviez *et al.*, 2015). The new *P. beebei* sequences were 623 bp in total length, but only a 530-bp region was used in the phylogeny reconstruction. For the latter sequence length the  $p$ -distance between *P. beebei* n. sp. and *Provanna* sp. SP-2014 (KJ566951) was 0.2%. Partial COI sequences (638 bp) of the nine specimens of *P. cooki* n. sp. consisted of two haplotypes that differed from each other by an uncorrected  $p$ -distance of just 0.2%. The three specimens sequenced from the same lot as paratype 3 represent both haplotypes; all three have a ribbed shell. One of the two haplotypes was dominant: it accounted for seven of the nine individuals sequenced by us and was represented in all three sequenced lots. These results confirmed the ‘smooth’ and ‘ribbed’ morphotypes as one molecular operational taxonomic unit (MOTU).

Both the Bayesian and ML analyses using a 530-bp alignment of the COI gene (Fig. 9) yielded similar relationships within the clade *Provanna* and strong support for the monophyly of all currently accepted genera. However, the two sets of analyses differed in the relative position of other abyssochrysoide genera (although all currently accepted genera were well supported in both) and in relationships within the genus *Alviniconcha*. The species of *Provanna* clustered in a single strongly supported clade within the Abyssochrysoidea; Bayesian posterior probability (PP) and ML bootstrap support (BS) values were 100% and 99%, respectively. The monophyly of both *P. beebei* n. sp. and *P. cooki* n. sp. was well supported (Fig. 9), and both species were well supported as distinct MOTUs; for *P. beebei* n. sp., PP and BS values were 100% and 99%, respectively, and for *P. cooki* n. sp., both support values were 99%. On the basis of the 530-bp COI region used in the phylogenetic analyses, the  $p$ -distance between the two new species was 4.5% (the corresponding  $p$ -distance for the total 638-bp region sequenced was 3.9%). *Provanna cingulata*, *P. beebei* n. sp. and *P. cooki* n. sp. together formed a well supported clade in both sets of analyses (PP = 98%; BS = 96%; Fig. 9).

## DISCUSSION

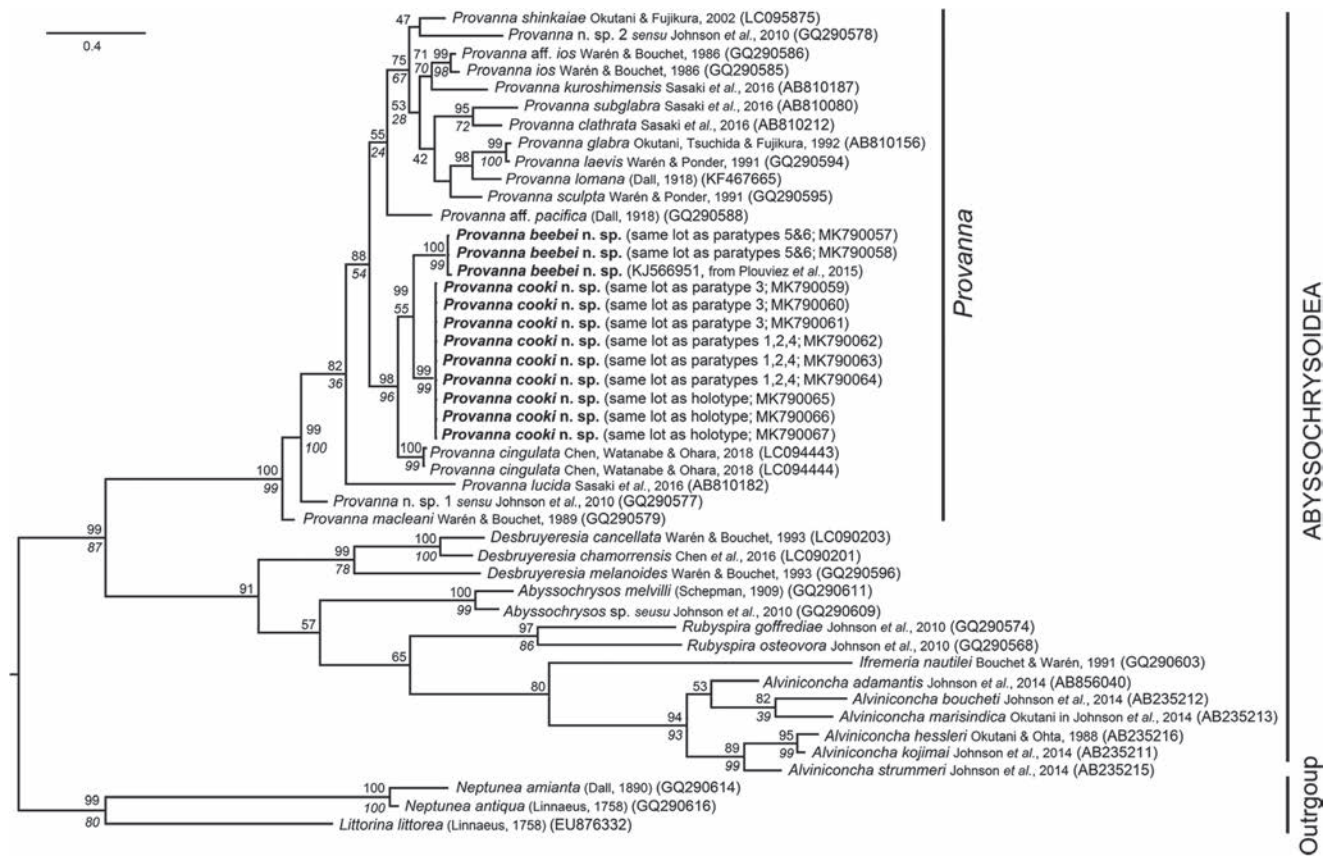
Taxonomic analysis of provannid gastropods from the Beebe Vent Field and the E2 and E9 vent fields of the East Scotia Ridge reveals two new species of *Provanna* that can be distinguished from each other and from previously described species by a combination of morphological and molecular features. Our work suggests that the specimen from the Cayman Trough sequenced in Plouviez *et al.* (2015) is conspecific with *P. beebei* n. sp. On the basis of partial COI sequence data, the two new species together with the Western Pacific species *P. cingulata* form a strongly supported clade.

*Provanna cooki* n. sp. exhibits considerable variation in shell morphology. Appreciable variation has been reported for *P. variabilis*



**Figure 8.** Shell-size frequency distributions for *Provanna beebei* n. sp. (A, B) and *P. cooki* n. sp. (C–I). A. Beebe Chimlets. B. Anemone Field. C. E2 Vent Field (all specimens). D. E9 Vent Field (all specimens). E. E2 Dog's Head. F. E9 Marsh Tower. G. E2 Deep Castle. H. E9 SW Field. I. E2 Diffuse. E2 was dominated by the smooth form of *P. cooki*, and only the ribbed form was collected from E9.





**Figure 9.** Bayesian phylogeny of *Provanna* within the Abyssochrysoidea, using partial COI sequences (530 bp). PP and BS (in italic font) values are shown above and below branches, respectively; BS values are not shown where there was conflict between Bayesian and ML analyses. The two sets of analyses differed in the relative position of abyssochrysoid genera and in relationships within the genus *Alviniconcha*. Scale bar indicates substitutions per site.

Warén & Bouchet, 1986, but this does not appear to follow any clear pattern (e.g. size-related variation in shell sculpture). The two morphotypes of *P. cooki* n. sp. differed in shell sculpture and were initially identified as two morphotypes by Rogers *et al.* (2012). The pattern observed for this species parallels that found in the stalked barnacle *Neolepas scotiaensis* at the E2 and E9 vent fields (Buckeridge, Linse & Jackson, 2013). The ‘smooth’ morphotype of *P. cooki* n. sp. and the ‘robust’ morphotype of *N. scotiaensis* occupy sites of low hydrothermal activity at the E2 vent field, whereas the ‘ribbed’ morphotype of *P. cooki* n. sp. and the ‘gracile’ morphotype of *N. scotiaensis* inhabit areas near the venting source at the E9 vent field. A lepetodrilid limpet, *Lepetodrilus concentricus*, is known from the vent sites at E2 and E9 as well as from the adjacent hydrothermally active Kemp Caldera; this showed an extraordinary range in shell dimensions between E2/E9 and the Kemp Caldera, but no variation in shell pattern was observed in relation to low and high venting habitats (Linse *et al.*, 2019).

*Provanna* belongs to the superfamily Abyssochrysoidea, a group that seems to display high morphological plasticity. Warén & Bouchet (1993: 74) remarked that the genus displays simple and highly variable shells, often with two morphotypes at the same site, and that this makes species identification difficult. Since Warén & Bouchet published their work, several species of *Provanna* have been described (Table 1), but intraspecific morphometric data comparable to the data obtained for *P. beebei* n. sp. and *P. cooki* n. sp. have not been available until now. The preliminary molecular systematic analyses presented here suggest that *P. cooki* n. sp. is represented by two distinct ecophenotypes. Thus, *P. cooki* may be a suitable species for further studies on the environmental and genetic drivers of plasticity in vent species. Since E2 was dominated by the smooth form and only the ribbed form was

present in E9, we speculate that variation in abiotic factors (e.g. temperature, levels of transition metals and sulphide) between E2 and E9 vent fields (Rogers *et al.*, 2012; Hawkes *et al.*, 2013; James *et al.*, 2014) may underlie the morphological differences observed. James *et al.* (2014) reported on the composition and concentration of hydrothermal fluids from diffuse flow sites at E2 and E9; these sites are located close to the sites where our *Provanna* samples were collected. Although the temperature of fluids in the habitat of *P. cooki* n. sp. at E2 (20 °C for diffuse flow below Dog’s Head chimney; 3.5 °C for Anemone Field) and E9 (5 °C for Marsh Tower; 20 °C for SW Field) were within a similar range, concentrations of some elements differed significantly between the E2 and E9 sites. These elements included Cs (3.5–26.5 nmol/kg at E2; 0.37–6.33 nmol/kg at E9), Mn (9.76–94.2 µmol/kg at E2; 0.82–18.9 µmol/kg at E9) and Fe (2.17–4.13 µmol/kg at E2; 0.0–5.4 µmol/kg at E9).

We found that *P. cooki* n. sp. showed spatial variation in size within the E2 and E9 vent fields. This kind of pattern has also been reported for *L. concentricus* and *Neolepas scotiaensis* from the same assemblages (Buckeridge *et al.*, 2013; Linse *et al.*, 2019). Spatial variation in size has also been found in other vent taxa. This has been explained in terms of size partitioning based on age or sex, as in the lepetodrilid *Lepetodrilus fucensis* (Bates, 2008; Kelly & Metaxas, 2008), the shrimp *R. hybisae* (Nye, Copley & Tyler, 2013b) and the alvinellids *Paralvinella palmiformis* and *P. hessleri* (Copley *et al.*, 2003; V. Nye & J. Copley, unpubl.), or by size differences in ecophenotypes, as has been reported in the tubeworm *Ridgeia piscesae* (Tunnicliffe, St Germain & Hilario, 2014) and the stalked barnacle *N. scotiaensis* (Buckeridge *et al.*, 2013).

The two new species reported here extend the known distribution of *Provanna* and provide the first records of the genus in the

Caribbean Sea and Southern Ocean. Although the vent fauna at the Mid-Cayman Spreading Centre appears to be largely distinct at the species level (Nye, 2014), the presence of shrimp-dominated faunal assemblages at both the Beebe and Von Damm vent fields supports higher-level taxonomic affinities with the Mid-Atlantic Ridge vent fauna (Connelly *et al.*, 2012; Nye, Copley & Plouviez, 2012; Plouviez *et al.*, 2015). However, the vent fauna of the Mid-Cayman Spreading Centre also exhibits faunal affinities with the West Pacific and other provinces (Nye, 2014; Plouviez *et al.*, 2015). While *P. beebei* n. sp. appears to be morphologically most similar to *P. macleani* from cold seeps and organic fall in the East Pacific, our COI-based phylogenetic analyses provided strong evidence that it forms a clade with the Southern Ocean *P. cooki* n. sp. and West Pacific *P. cingulata*. Understanding the evolutionary origins of these complex biogeographic patterns and the biogeographic affinities of the vent fauna of the Mid-Cayman Spreading Centre will be a challenging task.

Biogeographic analyses suggest that while the East Scotia Ridge vent fauna represents a distinct biogeographic province with unique faunal elements, a component of this fauna is shared with vents in the west and southwest Pacific and the Mid-Atlantic Ridge (Rogers *et al.*, 2012; Nye, 2014). The discovery of a new species of *Provanna* at vent sites on the East Scotia Ridge suggests that the environmental conditions of the Southern Ocean do not act as a barrier for this genus and highlights the unique species composition of the faunal assemblage in this vent biogeographic region.

The recent exploration and investigation of hydrothermal vent fields in the Caribbean and Southern Ocean have enhanced our knowledge of biodiversity in the deep sea and the biogeography and evolutionary history of vent fauna. The discovery of two new species of *Provanna* underscores the existence of undiscovered biodiversity in off-axis vents and in Antarctic and deep-sea settings. Our phylogenetic analyses, which were based on a single mitochondrial gene region, were unable to fully resolve phylogenetic relationships within *Provanna*. A multigene analysis is required to elucidate the phylogenetic and biogeographic relationships of recent *Provanna* species.

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