



Discovery and description of a remarkable bathypelagic nudibranch, *Bathydevius caudactylus*, gen. et. sp. nov.

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ABSTRACT

We describe an exceptional nudibranch, new to science, from bathypelagic depths in the eastern North Pacific Ocean. More than 100 individuals of *Bathydevius caudactylus* gen. et. sp. nov. have been observed in the water column at depths between 1013 and 3272 m. Twenty spawning individuals were observed on the seafloor at depths between 2269 and 4009 m. Anatomy, diet, behavior, bioluminescence, and habitat distinguish this surprising nudibranch from all previously described species, and genetic evidence supports its placement in a new family.

1. Introduction

Nudibranchs are “naked snails” (Ricketts and Calvin, 1952) that occur over a broad range of latitudes from the tropics to polar seas. These gastropods are known principally from lower intertidal and subtidal habitats as colorful and sometimes whimsically named (e.g., Spanish Dancer, White Knight, Sea Clown) predators of sessile cnidarians, sponges, and bryozoans (Morris et al., 1980; Ricketts et al., 1985). They can also be found living holopelagically in the ocean’s uppermost layers (Lalli and Gilmer, 1989), at the air-sea interface (Bieri, 1966), and on the deep seafloor at depths exceeding 4000 m (Valdés, 2002a). They have not been previously reported to inhabit the deep water column.

The ocean’s deep midwaters comprise the largest living space on Earth, and as we explore them with advanced technologies, we continue to find novel and unexpected life forms. Adaptation to the deep pelagic habitat can yield striking transformations of familiar body forms and natural histories among taxa commonly found at shallower depths (Robison et al., 2005; Harbison et al., 2001; Madin and Harbison, 1978). These discoveries serve to reinforce concerns about the consequences of exploiting natural resources from deep oceanic regions that are poorly explored and insufficiently understood (Robison, 2009; Drazen et al., 2020). The adaptations that allow animals to succeed in this cold, dark realm can tell us a great deal about the ecology and sustainability of Earth’s least known major habitat. Here we describe a remarkable nudibranch that occurs at bathypelagic depths in the eastern North Pacific

Ocean (Fig. 1).

2. Materials and methods

2.1. Sample collection and in situ observations

The principal study area was at 36.3° N, 122.9° W; off central California, where the 3500 m isobath crosses the axis of the Monterey Submarine Canyon, about 90 km west of Point Sur (Robison et al., 2010). A map and hydrographic profile are presented in Supplementary Figs. S1 and S2.

We used MBARI’s (Monterey Bay Aquarium Research Institute) deep-diving, remotely operated vehicles (ROVs) Tiburon and Doc Ricketts to make observations *in situ* and to collect specimens (Robison et al., 2017; see supplementary material: methods). Real-time observations were conducted and recorded with high-resolution, HD color video systems. Overall, we made extended in-situ observations (up to 2 h each) of 32 individuals. Eighteen specimens were collected for further investigation from the same area. Specimens were collected with 6.5 L “detritus” samplers (Robison, 1993; Youngbluth, 1984) and were brought up to the shipboard laboratory. Captured specimens were maintained in temperature-controlled, environmental chambers aboard the R/V Western Flyer and ashore. In the laboratory at sea, specimens were held at 3°–4 °C and in the dark, except during examination. Despite gentle capture techniques and careful handling during recovery, most

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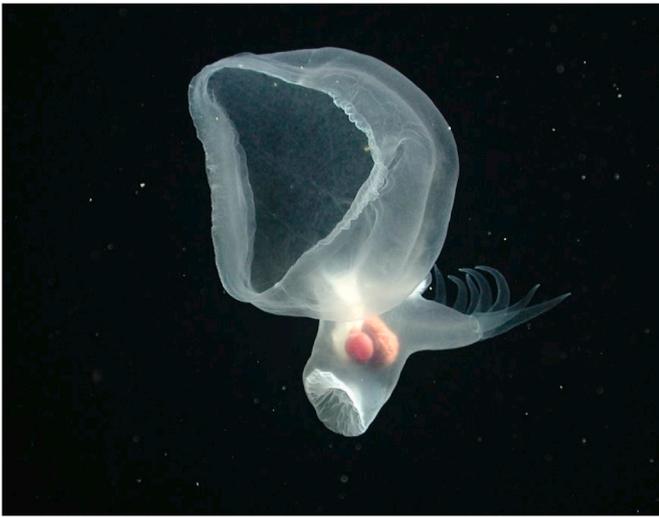


Fig. 1. *Bathydevius caudactylus* gen. et. sp. nov. in situ, from a video frame grab.

specimens arrived at the surface either moribund or unresponsive. Light-microscope examinations and dissections were made on fresh material at sea and on preserved material ashore. Digital images of anatomical regions were examined and recorded from both living and preserved material.

Video footage recorded by MBARI's ROVs at depth is initially annotated in real time, and then again in detail ashore after a dive series. Environmental data, linked to the video time code, are archived in a database that can be accessed for individual or cumulative information on: depth of occurrence, hydrographic conditions (e.g. temperature, O₂ level, salinity, etc.), hydrographic season, and co-occurring species. An information management system (VARS) allows searches within the database for specific annotation terms and facilitates the ready retrieval of video sequences for examination (Schlining and Stout, 2006). These systems allowed us to readily re-examine our field observations, select individual video frames and sequences for inspection of structure and movement, and to search the database for patterns and conditions of occurrence.

2.2. Oxygen consumption measurements

Respiration, as a proxy for metabolism, was measured *in situ* with a novel instrument developed at MBARI. The system is carried to depth by an ROV where single specimens are placed in one of eight individual chambers fitted with optodes (Bittig et al., 2018) to continuously measure oxygen levels. The ROV then transfers the instrument to a mooring at a depth comparable to that at which the specimens were collected, and the system is allowed to incubate for periods up to 72 h. An onboard computer records the data from eight chambers and controls periodic flushing to allow repeated runs. At the end of each deployment, the MRS (Midwater Respirometry System) is recovered by the ROV and returned, with the specimens, to the surface.

2.3. DNA extraction and sequencing

DNA from flash-frozen specimens was extracted using a Qiagen DNEasy kit, and we Sanger-sequenced three genes (18S and mitochondrial 16S and COI) from two specimens collected on separate expeditions two months apart (MBARI Dive and Sample Numbers D0089-D1, D0105-SS2). For outgroup analyses, we also sequenced five specimens of the pelagic nudibranch *Phylliroe* for 18S and one specimen for COI. GenBank accession numbers and specimen details for all these new sequences are listed in [Supplementary Table S1](#).

Mollusc sequences obtained from GenBank via Entrez searches and

bioprojects had their names cleaned, redundant sequences removed, and were aligned with mafft using options `-maxiterate 1000 -localpair`. Trees were estimated using raxml-ng with parameters `-all -bs-trees 100 -model GTR + G`, specifying the outgroup as *Littorina* for COI and *Mytilus* for 16S and 18S. We also used IQTree with parameters `-m TEST-bcon 100` to determine the best model for each gene (18S: TIM2+F+I+G4; 16S: TVM+F+I+G4; COI: GTR+F+I+G4). The position of *Bathydevius* relative to other gastropods was identical with both tree-inference programs (not shown). To avoid over-interpretation of poorly supported topologies, we collapsed nodes with less than 50% support, using the function `as.polytomy` from the R package *ape* (Paradis et al., 2004), and resultant trees were visualized using FigTree (github.com/rambaut/figtree/). All raw trees and collapsed trees are for the three genes are presented as [Supplemental Figures \(S7-S13\)](#). Sequences are registered in GenBank ([Table S1](#)), and the taxonomy in ZooBank (LSID:urn:lsid:zoobank.org:pub:FCD1D6B2-BB9B-46E8-8C0A-684B3F61C9F5). Sequence alignments used to generate trees are available in DataDryad to doi.org/10.5061/dryad.3bk3j9kvp.

3. Results

We encountered a total of 157 individuals of the new nudibranch during ROV dives, year-round, between the years 2000 and 2021. One hundred thirty-seven of these were found in the water column at depths between 1013 and 3272 m (average = 1989 m) (supplementary material, [Fig. S4](#)). These midwater individuals occurred within a temperature range of 1.6–2.8 °C (average = 2.2 °C), and ambient oxygen concentrations ranged between 0.8 and 2.8 ml/L (average = 1.5 ml/L). Twenty individuals were observed on the seafloor at depths from 2269 to 4009 m (average = 3439 m). The benthic individuals occurred at temperatures between 1.5 and 1.8 °C (average = 1.6 °C) and at oxygen levels from 1.6 to 2.7 ml/L (average = 2.3 ml/L). All midwater individuals were solitary, while some of the benthic individuals were found in proximity to each other.

Most of the individuals were observed in the vicinity of our deep, midwater survey site (36.331N, 122.901W) in the Monterey Submarine Canyon off central California (Robison et al., 2010). We observed additional individuals off the coast of Oregon (45.134 N, 125.848 W), in the waters over the Davidson Seamount (35.749 N, 122.717W), and 320 km northwest of Point Conception (35.145 N, 122.948 W). Two individuals that appear to be *Bathydevius* were video-recorded by an ROV during a NOAA cruise in the western Pacific (Cantwell et al., 2017). The size range of the specimens that we collected was between 56 and 145 mm in length, measured from the apex of the oral hood to the tip of the longest projection on the tail.

3.1. Systematics

Class GASTROPODA.
Subclass HETEROBRANCHIA.
Order NUDIBRANCHIA
Suborder incertae sedis.
Family Bathydeviidae fam. nov.
Bathydevius gen. nov.
caudactylus sp. nov.

3.2. Type material

The holotype ([Fig. S3](#)) and two paratypes are deposited in the Smithsonian Institution's U.S. National Museum of Natural History (holotype: USNM 1740705, paratypes: USNM 1740706, 1740707). The holotype was collected at a depth of 1566 m at MBARI's deep midwater site (36.33°N, 122.89°W; where the seafloor depth is 3500 m) off Monterey Bay during ROV Tiburon dive 649 on January 29, 2004. Paratypes were collected from the same locality and at comparable depths, over a 5-year span. All types are undissected and preserved in

ethanol.

3.3. Etymology

The generic name *Bathydevius* gen. nov. describes a deep-living deviation, to reflect its diversion from the evolutionary path of its relatives in appearance, molecular signature, and natural history. The species name *caudactylus* sp. nov. refers to the finger-like projections that line the posterior margin of the tail.

3.4. Diagnosis

Bathydevius caudactylus gen. et. sp. nov. (Fig. 1) is a mostly

transparent, gelatinous nudibranch composed of three distinct regions: the head, supporting a voluminous, bell-shaped oral hood; a body enclosing the internal organs and bearing the columnar ventral foot; and a spatulate tail fringed with 9–16 caudal appendages “dactyls.” The dorsal surface has two stubby, unsheathed rhinophores and a gently curved ridge of gills with the anal opening just posterior to the center of the gill ridge. Ventrally, the body merges into a short, cylindrical foot. Visible through the transparent body, the stomach is typically red, the rugose digestive gland is orange or brown, and in mature individuals, gonadal tissue on the right side of the digestive gland is opaque white.

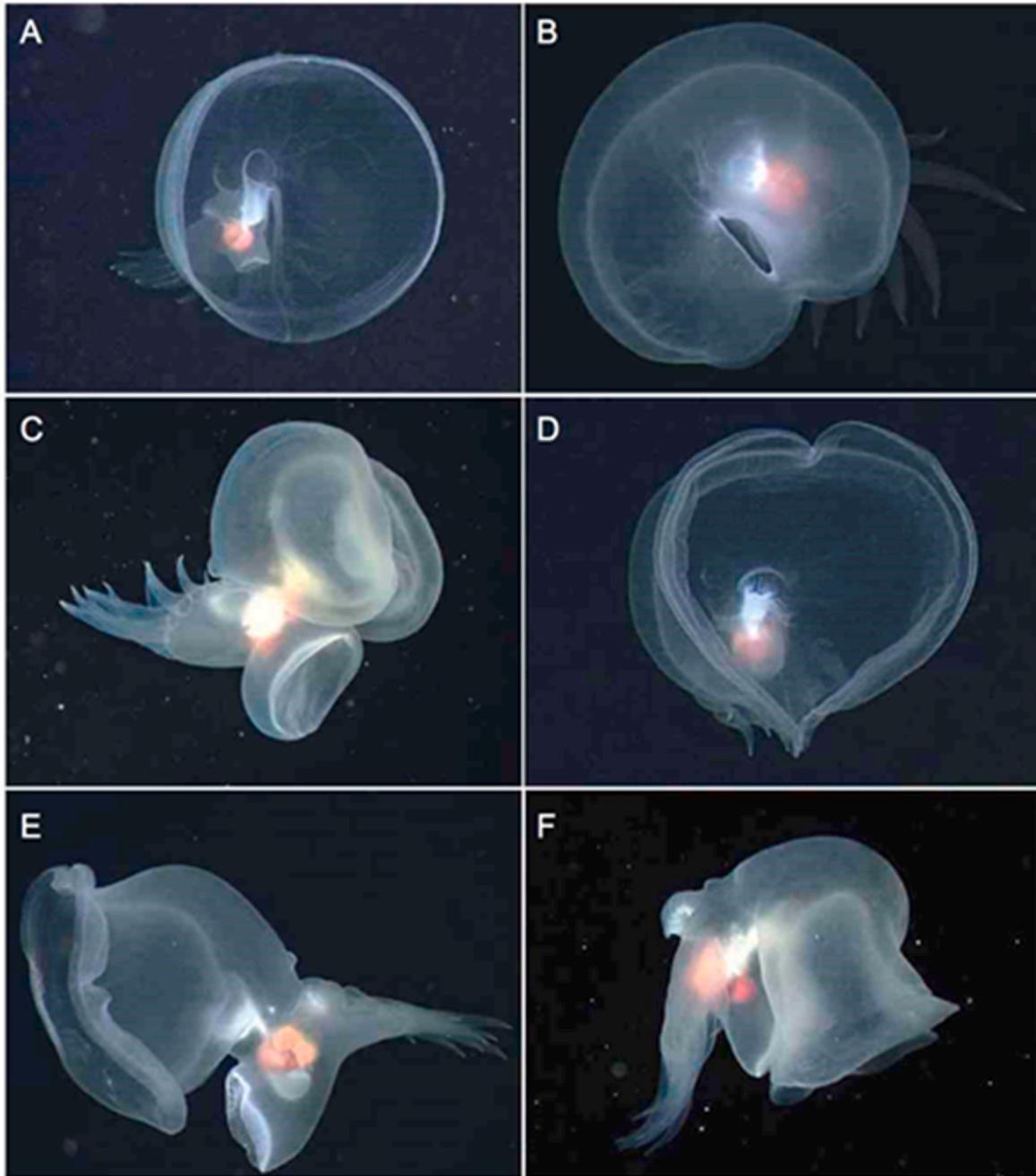


Fig. 2. Hood configuration modes for *Bathydevius caudactylus* gen. et. sp. nov.: (a) fully expanded; (b) the hood is closed around an open sphincter; (c) the hood is bilobed, closed along its vertical axis; (d) invagination in the upper margin with a pinched projection in the lower margin; (e) the peripheral lip of the hood is rolled back against the outer surface of the bell; (f) in a propulsive pulse.

3.5. Description

Specimens ranged in size from 56 mm to 145 mm, measured from the dorsal apex of the oral hood to the tip of the tail's central dactyl. Measurements from the largest specimen are indicative of the general proportions of pelagic adults: hood diameter = 89 mm; distance between rhinophores = 36 mm; width of gill ridge = 19 mm; greatest tail width = 60 mm; tail length = 31 mm; foot diameter = 26 mm; base of foot to top of gill ridge = 48 mm; smallest dactyl = 3 mm; longest dactyl = 34 mm. In the smallest, immature specimens, the body was very short, the internal organs occupied the body from the rear of the hood into the base of the tail, and the distinctions between the three regions of the body were less pronounced than in the adult.

3.5.1. External morphology

There are three integral regions: the head, the body, and the tail. The head is dominated by the oral hood, which is highly elastic. In its relaxed state, the hood is bowl-shaped with thick, muscular walls. The mouth is located at the back of the hood, just below the medial centerline (Fig. 2a). The lip of the hood is very flexible, with annular and radial bands of muscle that allow it to close as a sphincter (Fig. 2b), or to close along the vertical axis (Fig. 2c). The dorsal-most part of the lip is nearly prehensile; it can peak to form a projection, or invaginate to form a notch in the margin of the hood (Fig. 2d). The lip can also be rolled back against the outer surface of the bell (Fig. 2e). The hood can be used to propel the animal backward, with a medusoid pulse during flexion (Fig. 2f).

The body, or trunk, is continuous with the posterior portion of the head. Its configuration is variable, depending on the activity of the animal. The rhinophores are located on the dorsal surface, widely separated to the left and right (Fig. S5); they are unshathed and non-retractile. A patch of opaque, pale tissue covers the top of each rhinophore. The gills are located centrally on the dorsal surface of the trunk, arching from an elevated ridge over the base of the tail (Fig. S5). Each gill element is a simple, convoluted plate without lamellae. The number of gill elements we found ranged from 8 to 15. The gills are non-retractile. The foot is cylindrical, extending ventrally from the mid-body below the gut. At its terminus is a concavity ringed by a thin band of muscle (Fig. 1).

The tail is rounded, broad and relatively flat, its base merges ventrally with the foot, and dorsally beneath the gill ridge. It can be flexed both dorsally and ventrally. Along the curved terminal margin of the tail are from 9 to 16 elongate conical projections ("dactyls"). In general, the smallest of these are at the outermost portion of the tail and they become progressively larger toward the midline. However, these structures are easily broken free and small ones, apparently regenerating, sometimes appear amidst large ones in the central portion of the series. At the distal tip of each dactyl is a cluster of opaque cells connected by a slender thread of what we assume to be nerve, to the center of a flat septum at the anterior end. There it forms multiple branches to connect with a ring of similar threads around the base, and from that junction it continues into a network in the tail. Some of these appendages may be forked along their length, terminating in two tips. On very small specimens (<65 mm) the longest dactyls have slender filaments (<2 mm) trailing from their tips. These filaments are filled with opaque cells.

3.5.2. Internal anatomy

The mouth is a broad, flexible funnel at the ventro-posterior region of the oral hood. It appears white/opaque because of numerous irregular, longitudinal folds that can expand to allow the passage of large prey. This opening tapers downward through a brief esophagus into the anterior of the rounded, bright red stomach, which connects dorsally to the digestive gland located just above it (Fig. 3). We found no distinct buccal mass and no radula. The inner surface of the stomach consists of regular, longitudinal ridges, which can spread apart to allow expansion.



Fig. 3. Internal anatomy of *Bathylodius caudactylus* gen. et. sp. nov. The red organ is the stomach, the rugose orange organ is the digestive gland, and the small white patch is the brain.

Between the stomach and digestive gland is a small, rounded caecum, the same color as the stomach. The caecum and the dorsal surface of the stomach fit into a hollow area in the ventral part of the digestive gland. The digestive gland is brick-colored, typically orange or brown, with a rugose outer surface that resembles a raspberry. The intestine is a slender tube that begins at the left side of the junction between the digestive gland and the stomach. It curves briefly forward then up and over the left side of the digestive gland and continues toward the dorsal surface of the body, where it terminates as a mid-line anal pore just beneath and behind the center of the gill ridge. The heart is a soft, transparent structure beneath the gills.

A convoluted genital duct extends from the right side of the digestive gland to the lateral surface of the body where it terminates in a single, monaulic opening that protrudes outward in ripe specimens. In immature specimens, only the empty ducting is apparent. In mature specimens there is a depression in the right side of the digestive gland, filled with a dome of transparent tissue that tapers out to the genital pore. In ripe specimens, the rugae on the right side of the digestive gland, and all of the gonadal tissue become swollen and bright white in color (supplementary material, Fig. S5). Two cup-like structures occur at the base of the genital duct, a curved one above it and a rounded one to the posterior. The penis rests within the lateral genital duct, sometimes protruding but most often withdrawn.

The brain is bi-lobed and sits in the dorsal portion of the body above the tapering esophagus, between the rhinophores and the gills (Fig. 3). Threads of nerve tissue spread outward from each lobe, most prominently to the tail, the oral hood, the rhinophores and the base of the foot.

3.6. Observations and measurements

3.6.1. Swimming/locomotion

The density of *B. caudactylus* must be nearly equal to that of seawater because when not swimming, it neither sinks nor rises. Swimming is achieved by dorso-ventral undulations involving the entire body from hood to tail. These actions move the animal forward in the direction of the long axis of the body. Rapid closure of the oral hood produces a medusoid pulse that, along with ventral flexion of the tail, can stop forward progress and move the animal backward. All observed motion except hood closure was very slow.

3.6.2. Feeding

The stomachs of 14 specimens were opened and all showed evidence of feeding on crustaceans. In some cases, this consisted of small pieces of chitin suspended in a slurry, or fragments of legs and antennae. In two

cases, partly digested but intact mysid shrimp, *Boreomysis californica*, were in the stomachs. Virtually every specimen we examined had a viscous red fluid in the stomach, typically containing microscopic chitin fragments.

3.6.3. Reproduction/spawning

On one occasion we closely observed two individuals of *Bathydevius caudactylus* on the seafloor, at a depth of 2755 m. They were within 2 m proximity of each other, and appeared to be spawning ribbons of eggs. For both, the distal end of the foot was greatly expanded as it gripped the substrate (Fig. 4). The animals were positioned so that their hoods faced downstream in the prevailing current. Their tails were raised up into the current while the dactyls trailed downstream around the trunk and hood. Both individuals were collected.

One of these specimens had two tails. The slightly larger left-side tail had 14 dactyls, with the smallest on the outside, the rest increased in length medially with the longest on the inside. On the right-side tail, there were 10 dactyls, again with the longest on the inside, closest to the midline. The second specimen had a single, asymmetric tail that was expanded on the right side. There were 15 dactyls overall, with a small one at the extreme left and the longest beside it; from left to right the remaining dactyls became progressively smaller. The gills and gill ridges on both of these specimens were larger, proportionally, than on specimens observed in the water column.

The genital pores of both benthic specimens were swollen and expanded. There were several folds of ribbon-like, white tissue in a pouch to the right of the white portion of the digestive gland. The pouch and the crenellated tissue continued through a curved cavity that terminated in a second opening through the genital pore. The stomachs of both benthic specimens were empty. Overall, 20 individuals were observed attached to the seafloor.

A rare specimen that made it to the surface alive was apparently ripe and when placed in an aquarium of chilled seawater it settled to the bottom. It produced a slender white ribbon of eggs that drifted, then attached to the bottom at one end of the tank. Within three days the ribbon matrix had dissipated and the eggs were released. The eggs developed within hours into holociliated trochophore larvae, with long cilia (supplementary material, Fig. S6).

3.6.4. Respiration

Oxygen consumption rates measured *in situ* for four specimens of *B. caudactylus* during three consecutive 12-h incubation periods for each individual; had a mean value of $0.005 \mu\text{MO}_2/\text{hr/gWW}$ at 2.13°C . This low level of respiration was roughly comparable to those of similarly-sized, cydippid ctenophores (*Bathyctena* sp.) and coronate



Fig. 4. *Bathydevius caudactylus* gen. et. sp. nov. on the seafloor in the posture associated with the release of an egg-bearing ribbon. Distance between the red laser dots is 29 cm.

scyphomedusae (*Paraphyllina ransoni*), measured during the same instrument deployments and thus at the same depths and temperatures (MBARI unpublished data). In contrast, the mean rate of four specimens of the typical prey, *Boreomysis californica*, again measured during the same deployments, were three orders of magnitude higher than that of the predatory nudibranch. The *in situ* respiration rates we measured for *B. caudactylus* are substantially lower than published rates for shallow-water nudibranchs (Havenhand and Todd, 1988; Caldwell and Donovan, 2003).

3.6.5. Bioluminescence

On two occasions, we recorded *in situ*, low-light video footage of individuals lit only by dim, red light. In one case, the animal began to glow blue across its dorsal surface, including the hood and dactyls. Light originated from small, embedded glowing granules which gave a starry appearance (Fig. 5), similar to what was later seen in the lab. On another occasion, a single dactyl began to glow brightly as it rotated and eventually detached from the animal, drifting apart.

We observed bioluminescence from twelve individuals in the lab. Undisturbed specimens did not produce light but upon gentle stimulation of the oral hood, blue light was produced at the points of contact. This luminescence spread as a diffuse glow through the transparent hood tissue. With more vigorous stimulation of the entire specimen, dozens of points of light appeared throughout the hood and at the tips and bases of the caudal dactyls. The luminescence persisted for 3–8 s after the stimulation ceased. No luminescence was produced by the tail or body in the lab specimens.

3.6.6. Molecular results

Sequences of the ribosomal 18S gene, and mitochondrial 16S and COI from two specimens of *Bathydevius caudactylus* and five specimens of *Phylliroe bucephala* were added to published sequences of other nudibranchs, gastropods, and molluscs, mainly derived from Hallas et al. (2017) and Wägele et al. (2003). A summary tree is shown as Fig. 6, and more complete trees are shown in supplementary Figures S7–S13. The three genes did not support exactly the same topology, although all three supported that *Bathydevius* is a divergent genus of Nudibranchia. Large subunit ribosomal 18S placed *B. caudactylus* as sister to the rest of cladobranch and dorida nudibranchs (Fig. 6, S7, S8, S11). In contrast, mitochondrial 16S and COI recovered *B. caudactylus* as sister to *Bathydoris* (Fig. 6, S9, S10, S12, S13).

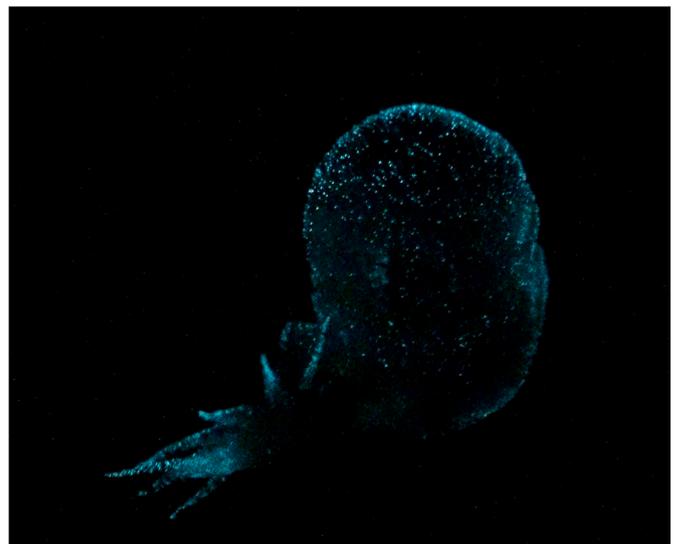


Fig. 5. Bioluminescence of *Bathydevius caudactylus* gen. et. sp. nov., recorded *in situ*. Light emanates from the surface of the oral hood and within the dactyls (at left).

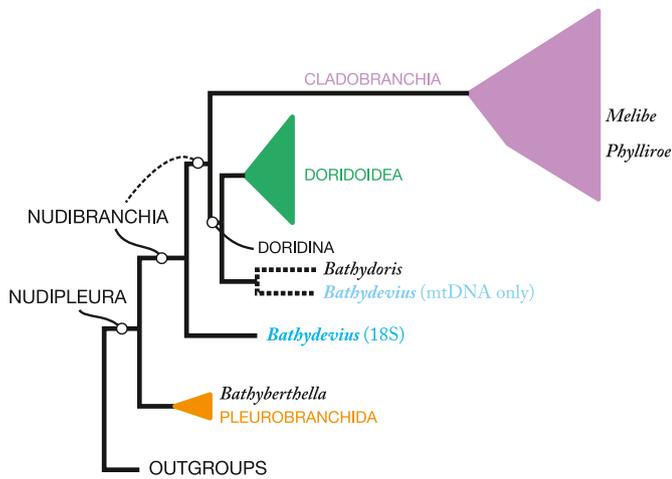


Fig. 6. Summary of molecular results placing *Bathydevius caudactylus* gen. et. sp. nov. near the base of the Nudibranchia clade. Using 18S, *B. caudactylus* appears as sister to the Cladobranchia and Doridina, while mitochondrial COI and 16S recover *B. caudactylus* as sister to the genus *Bathydoris*, albeit as part of a large unresolved polytomy. This molecular ambiguity is reflective of its morphological affinities to both dorids and cladobranchs. *Melibe* is clearly distinct from *Bathydevius*, supporting a convergent morphology. We have repositioned the node of the Nudibranchia to accommodate its inclusion (solid line), and the original designation is shown as a dashed line. For a summary tree showing bioluminescent lineages, see [Supplementary Fig. S7](#), and for complete 18S, 16S, and COI trees, see [Supplementary Figs. S8–S13](#).

4. Discussion

Bathydevius caudactylus is clearly adapted for pelagic life and is the first nudibranch to be reported from the vast bathypelagic habitat. The other open ocean nudibranchs, most recorded as plankton or neuston in near-surface waters, are either phylliroids (suborder Dendronotacea), glaucids, or fionids (suborder Cladobranchia) (Lalli and Gilmer, 1989). Sightings have been made of the phylliroids *Cephalopyge* and *Phylliroe* by MBARI's ROVs as deep as 1000 m but are not yet reported in the literature.

All previously known pelagic nudibranchs feed on pelagic cnidarians (Lalli and Gilmer, 1989). Preying on crustaceans is uncommon among nudibranchs and thus it is noteworthy that the subtidal tethydid *Melibe leonina*, which also has a large oral hood, feeds principally on crustaceans (Morris et al., 1980). Like *B. caudactylus*, *M. leonina* lacks a radula (Gosliner and Smith, 2003), but morphological similarity appears to be an example of convergence, and the two are widely unrelated given our molecular results. Another nearshore benthic, tethydid with an oral hood and no radula, *Tethys fimbria*, also feeds on crustaceans that it traps against the seafloor (Cimino and Ghiselin, 1999). Many unrelated midwater taxa have adaptations to entrap and passively subdue prey in a voluminous enclosure, including ctenophores, doliolids, and scyphomedusae (Robison et al., 2005; Swift et al., 2009; Larson et al., 1988), and this degree of convergence is one of the hallmarks of niche differentiation in the deep sea (Supplementary Fig. S14).

The low respiration rate we measured and the slow pace of life we observed *in situ* are common to a number of other bathypelagic taxa (Childress, 1995). The depth range inhabited by *B. caudactylus* is well below the deepest penetration of sunlight and the light regime there is based solely on bioluminescence. While some nudibranchs utilize aposematic coloration, others are cryptically colored to resemble their surroundings (Morris et al., 1980; Cunha et al., 2018). Transparency confers near invisibility to a great many deep-living animals and when only blue ambient light is available, red-based colors appear black (Johnsen, 2005). As a consequence, *B. caudactylus* is probably well protected from the few visually-cued predators that range through the bathypelagic.

In addition to its slow metabolism, a critical adaptation by *B. caudactylus* that allows it to succeed in deep water, where meals may be few and far between, is the shift to a prey that is very rich in nutrients. The key question is how do they catch their strong-swimming prey? From our observations and our own efforts to capture them, we know that the mysid *Boreomysis californica* is a powerful tail-flipper with a hair-trigger escape response.

The function of the finger-like dactyls on the tail of *B. caudactylus* remains obscure. They are not likely to be cerata because there is no apparent connection to the digestive tract, and the presence of a dorsal gill ridge would seem to preclude a respiratory function for the dactyls. We found no nematocysts in their tips, as can be the case in some aeolid nudibranchs. In some respects, they resemble the projections found on the tails of certain heteropod molluscs (Lalli and Gilmer, 1989), but the purpose of those structures is also unknown. They also call to mind the small tentacles that ring the oral hood of the highly derived, subtidal nudibranch *Melibe leonina*, which are known to aid in sweeping prey into the hood; but in the present case, they are at the wrong end of the animal for that job. Simultaneous flexion of the hood and tail would not allow these projections to propel food into the hood because the foot is in the way.

Given our *in situ* observations, their bioluminescent output, and the ease with which they are broken off the tail and then regenerate, the dactyls may function as autotomous, glowing distractions to predators. Autotomy of various body parts is known in other nudibranchs (Bickell-Page, 1989; Miller and Byrne, 2000), and bioluminescence has been reported in a few (Gosliner and Vallès, 2006). Another conceivable function is that the luminous dactyls are lures for prey.

Up to now, there have been two known independent lineages of bioluminescent nudibranchs: several genera of Polyceridae (Gosliner and Vallès, 2006), and *Phylliroe* (Herring, 1987) (supplementary Fig. S7). *Bathydevius* represents a third independent evolution of bioluminescence within Nudibranchia, and the seventh evolution of bioluminescence within gastropods. The other four gastropod lineages are terrestrial, freshwater, or parasitic clades, and are placed schematically into our tree given their distant relationships (supplementary Fig. S7).

All other pelagic nudibranchs, indeed all known opisthobranch molluscs, are hermaphrodites, which lay egg masses that yield a free-swimming veliger stage (Lalli and Gilmer, 1989). A penis was prominent on many of the mature pelagic specimens we examined. Both eggs and a penis were present in our benthic specimens, which suggest that simultaneous hermaphroditism is also the case for *B. caudactylus*. In the vast deep-sea habitat, this strategy would maximize the chances for reproductive success in an eremitic species.

In addition to the molecular data, which are sufficient alone, other lines of evidence reinforce our conclusion that *B. caudactylus* is neither a dorid nor an aeolid. Although the presence of an oral hood and a diet of crustaceans might suggest an affinity to a cladobranch like *Melibe*, which it somewhat resembles, we conclude that these similarities are examples of convergence, as discussed above. Dorid-like characteristics include an unbranched digestive gland, a branchial plume around the anus, and the lack of a radula. However, the combination of anatomy, diet, behavior, habitat, and molecular evidence distinguish this nudibranch from all others described to date.

Interpretation of molecular results: although the three gene trees presented here were not in complete accord, they all supported a unique designation for *Bathydevius caudactylus* at or near the base of the Nudibranchia. With mitochondrial genes, it was sister to *Bathydoris* which has typically been considered the sister group for suborder Doridina (Havenhand and Todd, 1988; Valdés, 2002a, 2002b). However, those genes produced essentially a polytomy (supplementary Figs. S9, S10), with extremely low support and signs of saturation. Therefore, we consider these genes are most useful for species-level distinction, whereas the 18S gene is more commonly used to infer family level relationships (Wägele et al., 2003; Valdés, 2002b).

In the context of the revised gastropod classification of Bouchet et al.

(2017), *Bathydevius* appears sister to the node which defines Nudibranchia (dashed line in Fig. 6), while remaining distinct from the Pleurobranchida. We would therefore expand this node to include *B. caudactylus* within the Nudibranchia. Assigning it to Doridina (based on mitochondrial sequences) would make that clade paraphyletic with Cladobranchia. There was no indication in any of the genes for even a remote relationship with *Melibe* — the other nudibranch with a similar feeding adaptation. Given these results and the many morphological differences from *Bathydoris* spp., it is justifiable to place the genus *Bathydevius* into its own family.

The deep waters of our oceans comprise the largest habitat on Earth (Angel, 2003; Haddock and Choy, 2024). They contain the largest animal communities on the planet, in terms of both biomass and numbers of individuals (Robison, 2004). Despite its obvious importance to the biosphere, the ocean's deep interior remains an unexplored frontier, more than a billion cubic kilometers of living space “that we have barely looked at and do not understand” (Kunzig, 2003). Within this enormous volume there are countless undescribed species, with biological adaptations and ecological relationships that we cannot yet imagine. A thorough evaluation of the risks to these communities from deep-sea mining and the extraction of both living and non-living resources should be conducted before such exploitation begins (Robison, 2009; Drazen et al., 2020).

5. Conclusions

In situ observations, collections, morphological and phylogenetic results confirm the presence of a population of bathypelagic nudibranchs in the eastern North Pacific.

CRediT authorship contribution statement

Bruce H. Robison: Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Steven H.D. Haddock:** Writing – review & editing, Validation, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dsr.2024.104414>.

Sequence alignments and software are available on Data Dryad at <https://doi.org/10.5061/dryad.3bk3j9kvp>

Data availability

Data will be made available on request.

References

- Angel, M.V., 2003. The pelagic environment of the open ocean. In: Tyler, P.A. (Ed.), *Ecosystems of the Deep Oceans*. Elsevier, Amsterdam, pp. 39–79.
- Bickell-Page, L.R., 1989. Autotomy of cerata by the nudibranch *Melibe leonina* (Mollusca): ultrastructure of the autotomy plane and neural plane and neural correlate of the behaviour. *Philos. Trans. Roy. Soc. Lond. B, Biol. Sci.* 324, 149–172. <https://doi.org/10.1098/rstb.1989.0042>.
- Bieri, R., 1966. Feeding preferences and rates of the snail, *Ianthina prolongata*, the barnacle, *Lepas anserifera*, the nudibranchs, *Glaucus atlanticus* and *Fiona pinnata*, and the food web in the marine neuston. *Publ. Seto Marine Biol. Lab.* 14, 161–170. <https://doi.org/10.5134/175429>.
- Bittig, H.C., Körtzinger, A., Neill, C., van Ooijen, E., Plant, J.N., Hahn, J., Johnson, K.S., Yang, B., Emerson, S.R., 2018. Oxygen optode sensors: principle, characterization, calibration, and application in the ocean. *Front. Mar. Sci.* 4, 429. <https://doi.org/10.3389/fmars.2017.00429>.
- Bouchet, P., Rocroi, J.-P., Hausdorf, B., Kaim, A., Kano, Y., Nützel, A., Parkhaev, P., Schrödl, M., Strong, E.E., 2017. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia* 61, 1–526. <https://doi.org/10.4002/040.061.0201>.
- Caldwell, S.L., Donovan, D.A., 2003. Energetics of swimming and crawling in the lion nudibranch, *Melibe leonina*. *Veliger* 46, 355–361.
- Cantwell, K., Pomponi, S., Fryer, P., 2017. Oceanographic Data and Information Collected during the EX1605L3 (CAPSTONE CNMI & Mariana Trench MNM) (ROV & Mapping) Expedition on NOAA Ship OKEANOS EXPLORER in the North Pacific Ocean from 2016-06-17 to 2016-07-10 (NCEI Accession 0156334); NOAA National Centers for Environmental Information. Silver Spring, MA, USA. <https://doi.org/10.7289/v5c24tqx>.
- Childress, J.J., 1995. Are there physiological and biochemical adaptations of metabolism in deep-sea animals? *Trends Ecol. Evol.* 10, 30–36. [https://doi.org/10.1016/S0169-5347\(00\)88957-0](https://doi.org/10.1016/S0169-5347(00)88957-0).
- Cimino, G., Ghiselin, M., 1999. Chemical defense and evolutionary trends in biosynthetic capacity among dorid nudibranchs (Mollusca: Gastroda: Opisthobranchia). *Chemoecology* 9, 187–207. <https://doi.org/10.1007/s000490050052>.
- Cunha, X., Viera, L.M., Migotto, A.E., 2018. Direct observations of the nudibranch *Corambe carambola* (Marcus, 1955) preying on the bryozoan *Alcyonidium hauffi* Marcus, 1939. *Mar. Biodivers.* 48, 1693–1694. <https://doi.org/10.1007/s12526-017-0664-9>.
- Drazen, J.C., et al., 2020. Midwater ecosystems must be considered when evaluating environmental risks of deep-sea mining. *Proc. Natl. Acad. Sci. USA* 117, 17455–17460. <https://doi.org/10.1073/pnas.2011914117>.
- Gosliner, T.M., Smith, V.G., 2003. Systematic review and phylogenetic analysis of the nudibranch genus *Melibe* (Opisthobranchia: Dendronotacea) with descriptions of three new species. *Proc. Calif. Acad. Sci.* 54, 302–355.
- Gosliner, T.M., Vallés, Y., 2006. Shedding light on the genera (Mollusca: Nudibranchia) *Kaloplacamus* and *Plocamopherus* with description of new species belonging to these unique bioluminescent dorids. *Veliger* 48, 178–205.
- Haddock, S.H.D., Choy, C.A., 2024. Life in the midwater: the ecology of deep pelagic animals. *Ann. Rev. Mar. Sci.* 16, 10.1–10.34. <https://doi.org/10.1146/annurev-marine-031623-95435>.
- Hallas, J.M., Chichvarkhin, A., Gosliner, T.M., 2017. Aligning evidence: concerns regarding multiple sequence alignments in estimating the phylogeny of the Nudibranchia suborder Doridina. *Roy. Soc. Open Sci.* 4, 171095. <https://doi.org/10.1098/rsos.171095>.
- Harbison, G.R., Matsumoto, G.I., Robison, B.H., 2001. *Lampocteis cruentiventer* gen. nov., sp nov: a new mesopelagic lobate ctenophore, representing the type of a new family (Class Tentaculata, Order Lobata, Family Lampoctenidae, fam. nov.). *Bull. Mar. Sci.* 68, 299–311.
- Havenhand, J.N., Todd, C.D., 1988. Physiological ecology of *Adalaria proxima* (Alder et Hancock) and *Onchidoris muricata* (Müller) (Gastropoda: Nudibranchia) I. Feeding, growth and respiration. *J. Exp. Mar. Biol. Ecol.* 118, 151–172.
- Herring, P.J., 1987. Systematic distribution of bioluminescence in living organisms. *J. Biolumin. Chemilumin.* 1, 147–163.
- Johnsen, S., 2005. The red and the black: bioluminescence and the color of animals in the deep sea. *Integr. Comp. Biol.* 45, 234–246. <https://doi.org/10.1093/icb/45.2.234>.
- Kunzig, R., 2003. Deep-sea biology: living with the endless frontier. *Science* 302, 991. <https://doi.org/10.1126/science.1090808>.
- Lalli, C.M., Gilmer, R.W., 1989. *Pelagic Snails: the Biology of Holoplanktonic Gastropod Mollusks*. Stanford University Press, Stanford, CA.
- Larson, R.J., Madin, L.P., Harbison, G.R., 1988. In situ observations of deep water medusae in the genus *Deepstaria*, with a description of *D. reticulatum*, sp. nov. *J. Mar. Biol. Assoc. U. K.* 68, 689–699. <https://doi.org/10.1017/S0025315400028800>.
- Madin, L.P., Harbison, G.R., 1978. *Thalassocalyce inconstans*, new genus and species, an enigmatic ctenophore representing a new family and order. *Bull. Mar. Sci.* 28, 680–687.

- Miller, J.A., Byrne, M., 2000. Ceratal autotomy and regeneration in the aeolid nudibranch *Phidiana crassicornis* and the role of predators. *Invert. Biol.* 119, 167–176. <https://doi.org/10.1111/j.1744-7410.2000.tb00005.x>.
- Morris, R.H., Abbott, D.P., Haderlie, E.C., 1980. *Intertidal Invertebrates of California*. Stanford University Press, Stanford, CA.
- Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20, 289–290. <https://doi.org/10.1093/bioinformatics/btg412>.
- Ricketts, E.F., Calvin, J., 1952. *Between Pacific Tides*, third ed. Stanford University Press.
- Ricketts, E.F., Calvin, J., Hedgpeth, J.W., Phillips, D.W., 1985. *Between Pacific Tides*, fifth ed. Stanford University Press.
- Robison, B.H., 1993. Midwater research methods with MBARI's ROV. *Mar. Technol. Soc. J.* 26, 32–39.
- Robison, B.H., 2004. Deep pelagic biology. *J. Exp. Mar. Biol. Ecol.* 300, 253–272. <https://doi.org/10.1016/j.jembe.2004.01.012>.
- Robison, B.H., 2009. Conservation of deep pelagic biodiversity. *Conserv. Biol.* 23, 847–858. <https://doi.org/10.1111/j.1523-1739.2009.01219.x>.
- Robison, B., Raskoff, K., Sherlock, R., 2005. Adaptations for living deep: a new bathypelagic doliolid, from the eastern North Pacific. *J. Mar. Biol. Assoc. U. K.* 85, 595–602. <https://doi.org/10.1017/S0025315405011525>.
- Robison, B.H., Sherlock, R.E., Reisenbichler, K.R., 2010. The bathypelagic community of Monterey Canyon. *Deep-Sea Res. II* 57, 1551–1556. <https://doi.org/10.1016/j.dsr2.2010.02.021>.
- Robison, B.H., Reisenbichler, K.R., Sherlock, R.E., 2017. The coevolution of midwater research and ROV technology at MBARI. *Oceanography* 30, 26–37. <https://doi.org/10.5670/oceanog.2017.421>.
- Schlining, B.M., Stout, N.J., 2006. MBARI's video annotation and reference system. In: OCEANS 2006. <https://doi.org/10.1109/OCEANS.2006.306879>.
- Swift, H.F., Hamner, W.M., Robison, B.H., Madin, L.P., 2009. Feeding behavior of the ctenophore *Thalassocalyce inconstans*: revision of anatomy of the order Thalassocalycida. *Mar. Biol.* 156, 1049–1056. <https://doi.org/10.1007/s00227-009-1149-6>.
- Valdés, A., 2002a. Phylogenetic systematics of '*Bathydoris*' s.l. Bergh, 1884 (Mollusca, Nudibranchia), with the description of a new species from New Caledonian deep waters. *Can. J. Zool.* 80, 1084–1099. <https://doi.org/10.1139/z02-085>.
- Valdés, A., 2002b. A phylogenetic analysis and systematic revision of the cryptobranch dorids (Mollusca, Nudibranchia, Anthobranchia). *Zool. J. Linn. Soc.* 136, 535–636. <https://doi.org/10.1046/j.1096-3642.2002.00039.x>.
- Wägele, H., Vonnemann, V., Wägele, W., 2003. Towards a phylogeny of the Opisthobranchia. In: Lydeard, C., Lindberg, D. (Eds.), *Molecular Systematics and Phylogeography of Mollusks*. Smithsonian Institution Press, Washington, DC, pp. 185–228.
- Youngbluth, M.J., 1984. Manned submersibles and sophisticated instrumentation: tools for oceanographic research. *Proc. SUBTECH* 1983, 335–344.