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Two new species of *Bargmannia* (Pyrostephidae, Physonectae, Siphonophorae)

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Abstract

Two new deep-living species of the genus *Bargmannia* (Siphonophorae, Physonectae, Pyrostephidae) are described based, almost exclusively, on the nectophores of single specimens collected by ROVs off the west coast of California. The nectophores of *B. stenotes* **sp. nov.** were relatively small, up to 11.4 mm in length and, in the preserved condition had very narrow nectosacs. There was a marked bend in the distal part of the preserved nectophore, resulting in the ostium opening upwards. The mature nectophores of *B. profunda* **sp. nov.** were almost twice as long as those of *B. stenotes* and were characterised by the fact that the lower lateral ridges did not join, distally, with the meso-lateral ones. This feature also was present in smaller nectophores of *B. amoena* but those of *B. stenotes*, at that stage, did not have a mouth-plate.

Key words: Siphonophorae, Physonectae, Pyrostephidae, Bargmannia, new species

Introduction

Pugh (1999) reviewed the genus *Bargmannia* and noted that Totton's (1954) original illustrations of *B. elongata* Totton actually referred to two *Bargmannia* species, and that he also had a third in his possession. There was very little possibility that Totton could have realised this fact as he was working with poorly preserved, net collected individual nectophores. The proof only came when more complete specimens were collected by submersibles, and later ROVs. Pugh gave fuller descriptions of both *B. elongata* and *B. lata* Mapstone, together with descriptions of two further new species, *B. amoena* Pugh and *B. gigas* Pugh, the last being based solely on some extremely large nectophores collected in a trawl.

Totton (1954) did not ascribe the genus *Bargmannia* to any family, but in his magnificent monograph (Totton, 1965) intuitively he placed it in the family Pyrostephidae, but gave no reasons for doing so. Pugh (1999) discussed this attribution and concluded that Totton was perfectly correct in doing so. He also mentioned some of the key characters that *Bargmannia* species shared with *Pyrostephos*, such as, for the nectophores, the ridge pattern, the muscle-free zone on the nectosac, and the lack of axial wings. There were also similarities in the tentilla and the possibility that *Bargmannia* species, like *Pyrostephos* might be dioecious. The molecular genetics studies of Dunn *et al.* (2005) showed that *Bargmannia* species were more closely related to known dioecious species than to the monoecious ones. Indeed, Munro *et al.* (2018), using transcriptome data clearly resolved the phylogenetic situation for the genus *Bargmannia*.

Dunn (2005) looked in detail at the colony-level organisation of *Bargmannia elongata*, and he drew attention to one important character in that the nectophores were attached on the opposite side of the stem to the siphosomal zooids, i.e. they were attached on the dorsal side as, by convention, the siphosomal zooids are considered to be attached to the ventral side. These details were discussed further by Pugh (2006), who noted that Pyrostephidae were the only family of the dioecious clade of physonects to possess a dorsal nectosome. This situation also enabled the genera of the family Agalmatidae to be clearly defined, as they too had a dorsal nectosome, but belonged to the monoecious clade.

In this paper two new deep-living species of *Bargmannia* collected in the vicinity of Monterey Bay will be described. Unfortunately, the descriptions will be based almost exclusively on the nectophores as most or all of the

siphosome probably became detached before collection, as has often been observed for several *Bargmannia* specimens found at such deep depths.

Bargmannia stenotes sp. nov.

Material examined: A single specimen collected by the ROV *Tiburon* Dive 674 that consisted of eight nectophores, a single bract, and a few gastrozooids and stem fragments. The specimen was collected at a depth of 3342 m on 22nd May 2004 at 35°55.15'N, 122°56.29'W. Two other specimens from the same region and similar depths may belong to this species (see below). Unfortunately, no frame grabs are available for this specimen.

Holotype: This specimen is designated the holotype and will be donated to the National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

Diagnosis. Small nectophores, up to 11.4 mm in length, with narrow nectosac tapering distally. In preserved state, the distal end of the nectophore was bent outwards so that ostium opened on upper side. Upper lateral ridges do not join with lower laterals proximally, but meso-laterals unite with lower laterals distally. Lateral radial canals arose, from upper canal, at some distance from pedicular canal. Leaf-like, thin bracts with distinctive lateral flap.

Description. *Nectosome*: No trace of the nectosomal stem was found with the specimen and so it can only be presumed, as is typical for other known *Bargmannia* species, that the nectophores were budded off on the dorsal side of the nectosome. The nomenclature for the various ridges on the nectophores has changed slightly from that used by Pugh (1999) as the terms apico- and infra-lateral have come to be considered inappropriate. Thus, as in Pugh & Baxter (2014), the apico-lateral ridges become the upper laterals, and the infra-laterals become the lower laterals. The meso-laterals remain unaltered.

Nectophores: A very young nectophore (Figure 1A) measured 1.45 mm in length and 1.3 mm width. It had a somewhat strange appearance as material seemed to have become attached to all the edges, making it look somewhat fuzzy. The upper, meso- and lower lateral ridges were very distinct, while the thrust block was barely developed. The ascending mantle canal was thick and very obvious. The nectosac was narrow, and was further constricted in its mid-region. There were no signs of a mouth-plate.

The other preserved nectophores were at various stages of development and measured up to 11.4 mm in length, 6.2 mm in width and 4.3 mm in depth. For a developing nectophore (Figure 1B), measuring 5.5 mm in length, the thrust block had considerably enlarged and on its lower side there was a deep median furrow. Proximally the ascending mantle canal inflected slightly into the mesogloea and formed a small swelling. Distally, it gave rise to a very short pedicular canal that, on reaching the nectosac, branched off only the upper and lower radial canals. The lateral radial canals arose, asymmetrically, from the upper canal at some distance from the pedicular canal. Either lateral canal could arise first. There was a large muscle-free zone on the proximal part of the lower surface of the nectosac. In the preserved state the distal end of the nectophore was bent upwards such that the ostium of the nectosac opened on the upper side of the nectophore. The nectosac itself, again in the preserved state, tapered down from its slightly emarginated proximal end and was very narrow distally.

The lower lateral ridges arose close to the proximal end of the thrust block and demarcated the lower lateral margins of the nectophore. Distally they merged with the meso-lateral ridges, on a level with the ostium, and together they continued below the ostium on either side of a small, broad mouth-plate. The upper lateral ridges did not extend down to meet them proximally, only merging with the meso-lateral ridges. They curved inwards on the upper side of the nectophore and then out lateral again. At that point they became much less prominent, and the two branches that each gave rise to were often difficult to detect. The inner branches ran to the top of the ostium and the outer pair curved round to reach its lateral margin in the region of a small lateral ostial process.

For the mature nectophores (Figures 2 & 3) the thrust block had increased further in size and occupied almost half the length of the nectophore. It was broad, only tapering in its proximal third, and its proximal end was formed by a digitate process that frequently was bent upwards. The ascending mantle canal arose below the tapering section of the thrust block and continued to about half the height of the nectophore. Typically, as noted in other *Bargmannia* species, it was slightly inflected into the mesogloea at its proximal end, and formed a small swelling. The nectosac, in its preserved state, was narrow and tapered down from its proximal end. As with the younger nectophore, its distal end was bent upwards so that the ostium of the nectosac opened on the upper side of the preserved nectophore. There was a large muscle-free zone on the proximal part of the lower surface of the nectosac that also spread, in the

central region, for a short distance onto the upper surface. In the middle of this zone, the very short pedicular canal gave rise to only the upper and lower canals. Again the lateral canals arose asymmetrically from the upper canal, at some distance from the pedicular canal. These ran obliquely to the sides of the nectosac and then ran directly to the ostial ring canal.

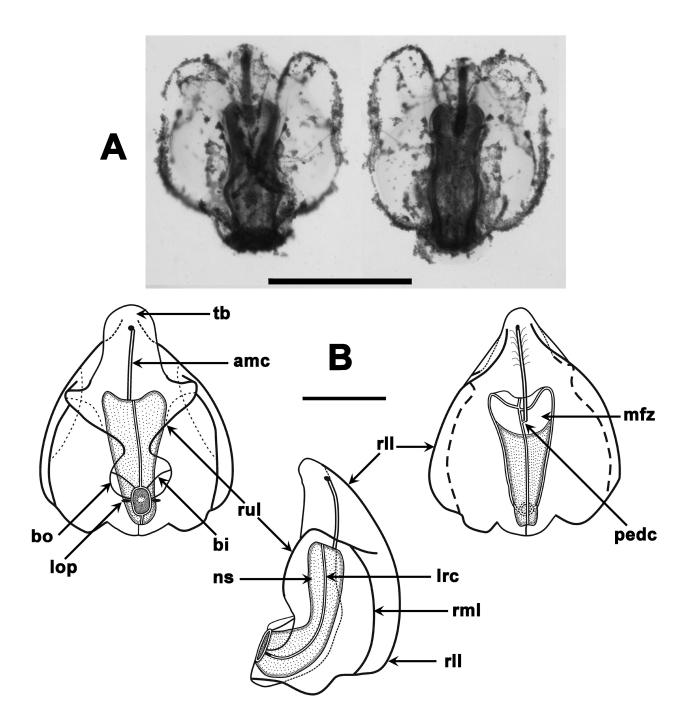


FIGURE 1. A. Very young nectophore of *Bargmannia stenotes* **sp. nov.**, upper side (left) and lower side (right). Scale bar 1 mm. **B.** Small nectophore of *Bargmannia stenotes* **sp. nov.** Upper (left), lateral (centre) and lower (right) views. **amc.** ascending mantle canal; **bi**, **bo**. inner and outer branches of upper lateral ridge; **lop**. lateral ostial process; **lrc**. lateral radial canal; **mfz**. muscle-free zone; **ns**. nectosac; **pedc**. pedicular canal; **rll**., **lrm**., **rul**. lower, meso- and upper lateral ridges; **tb**. thrust block. Scale bar 2 mm. Proximal at top, distal at bottom.

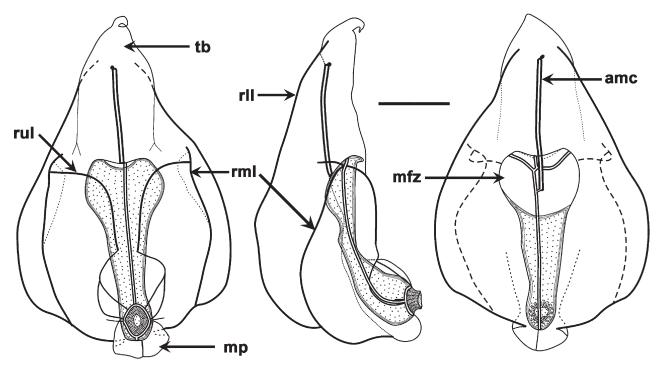


FIGURE 2. Mature nectophore of *Bargmannia stenotes* **sp. nov.** Upper (left), lateral (centre) and lower (right) views. **mp.** mouth-plate; for other annotations see Figure 1. Scale bar 2 mm.

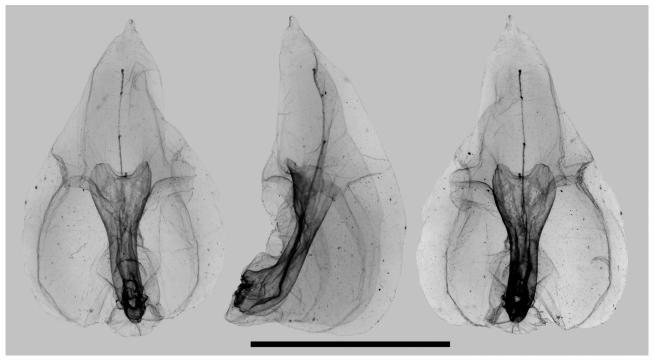


FIGURE 3. Photographs of one of the preserved nectophores of *Bargmannia stenotes* **sp. nov.** Upper (left, lateral (centre) and lower (right) views. Scale bar 5 mm.

The arrangement of the ridges remained the same as in the younger nectophore with the upper laterals not joining with the lower ones. The lower lateral edge of the nectophore was distinctly emarginated in the region where the lower laterals ridges merged with the meso-laterals ones. The mouth-plate was now well-defined although remaining relatively small. It was either rounded or very slightly emarginated in the mid-line. The lower nerve tract could distinctly be seen running over it. The lateral ostial processes were reduced to short, narrow strips.

Siphosome: As noted above the parts of the siphosome that were preserved consisted of only a single bract; three gastrozooids and some tangled tentilla.

Bract: The single bract (Figure 4A) that was found with the nectophores measured 5.5 mm in length and 4 mm in maximum width. It was thin and leaf-like. Although the edges were irregular the only clear character was a small flap from the upper side of the bract that hung out laterally on the inner side. The bracteal canal did not reach either end of the bract, and arose from a distinct indentation on the inner side of the bract. Until further, more complete specimens are collected one cannot be certain that this bract actually belongs to Bargmannia stenotes sp. nov.

Gastrozooid and tentacle: The larger gastrozooid measured 3.5 mm in length (Figure 4B) and featured an enlarged and distinctive basigaster, from which arose the tentacle of which only remnants remained.

Tentilla: The tangled mass of tentilla (Figure 4C) proved difficult to study, and all that will be remarked upon was the uncoiled cnidoband, and a long terminal filament. As is usual for *Bargmannia* species a few stenotele nematocysts, measuring c. 60 μm in length and 48 μm in diameter were present, but the remainder of the cnidome was not investigated. However, the large cells present on the terminal filament (see Figure 4C) were not nematocysts.

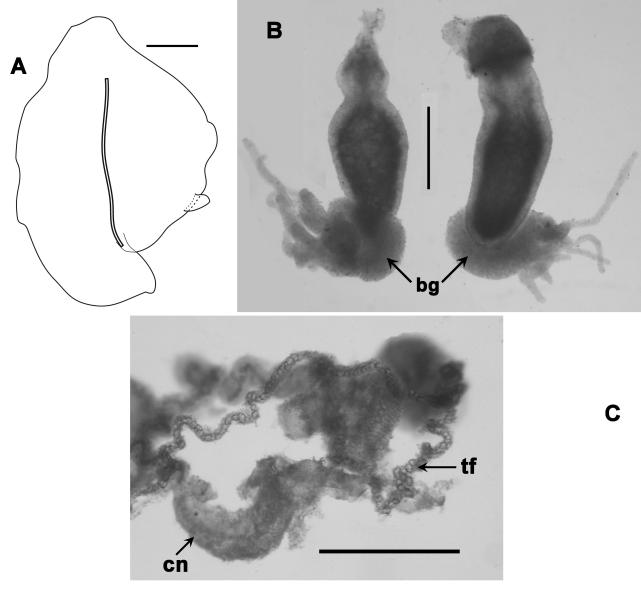


FIGURE 4. Bargmannia stenotes **sp. nov. A**. Possible bract. Proximal end at bottom; **B**. Gastrozooids. **C**. Tentilla. **bg**. basigaster; **cn**. cnidoband; **tf**. terminal filament Scale bars1 mm.

Remarks. Although this description is based on a single, very incomplete specimen there are certain characters that establish the specimen as a new species. Firstly, the single bract is very distinctive. There is, of course, the possibility that this single bract did not belong to the species being described, but evenso the morphology of the

nectophores is sufficient to distinguish the specimen as a new species. Thus, for instance, the mature nectophores were much smaller than those of all the presently described species. The longest nectophore of *Bargmannia stenotes* **sp. nov.** measured 11.4 mm, while according to Pugh (1999) the maximum for *B. amoena* was 19 mm, although for that species there was a very large range of sizes that might indicate that there is more than one species involved. *B. elongata* Totton averaged 21.3 mm and *B. lata* nectophores ranged between 14.79 and 31.94 mm in length. Nonetheless, the extreme narrowness of the nectosac is another characteristic feature as is the extent and shape of the thrust block. This is reflected by the high ratio between the total length of the nectophore and that of the nectosac, i.e. c. 1.90, compared with the next highest, 1.67, for *B. lata*. The marked bend in the distal part of the preserved nectophore, resulting in the ostium opening upwards, is also very characteristic, as is the fact that the upper lateral ridges do not join the lower lateral ones. *In toto* these characters appear sufficient to establish the specimen as a new *Bargmannia* species.

Two other *Bargmannia* specimens were collected at similar depths, in the vicinity of Monterey Bay, that might also belong to this species, both from *Doc Ricketts* Dive 666 (19th September 2014, 36°15'N, 122°09.99'W). One of these, from a depth of 3453 m, had just six nectophores in an extremely poor condition. The other, collected at a depth of 3172 m, consisted of thirteen nectophores, also in a poor condition, and two minute bracts. The nectophores were slightly larger than those of the holotype specimen of *B. stenotes* **sp. nov.**, and rather than just the ostial region, in the preserved state, being bent outwards, the nectophore was distinctly bent in it mid-region, giving the ascending mantle canal a distinctly arced appearance. Although the nectophores of these two specimens closely resembled those of *B. stenotes* **sp. nov.**, there was insufficient evidence to be certain that they belonged to that species.

Distribution. The type specimen was collected just north of the Davidson Seamount, California, U.S.A. at a depth of 3342 m.

Etymology. The Greek *stenotes*, meaning narrowness, refers to the narrowness of the nectosac in the nectophores.

Bargmannia profunda sp. nov.

Material examined: The specimen from ROV *Doc Ricketts* Dive 26 consisted of just nine nectophores. The specimen was collected at a depth of 3323 m on 27th May 2009 at 35°07'N, 122°46.5'W, off California, U.S.A.

Holotype: The above specimen is designated the holotype and will be donated to the National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

Diagnosis. Known only by its nectophores that measured up to 20.7 mm in length. Lower lateral ridges do not combine with meso-laterals distally. No mouth-plate. Nectosac relatively narrow and resembling a flattened cylinder. Triangular thrust block occupying almost half the length of the nectophore.

Description. An *in situ* frame grab was taken of the specimen (Figure 5). This shows that before collection the specimen had lost almost all of its siphosome and this could explain why no siphosomal zooids were preserved. There were no signs of any pigmentation.

Nectophores: The nine preserved nectophores varied in size from 11.8 mm in length and 6.7 mm in width to 20.7 mm and 12.3 mm, respectively. The ratio of the total length of the mature nectophore to that of the nectosac averaged 1.4. Although fairly robust, several of the preserved nectophores had lost the ectodermal lining to their nectosac, and in all others it was damaged. Although collectively it was possible to trace the arrangement of the radial canals, it was very difficult to discern the extent of the muscle-free zone on the lower side of the nectosac, and it may be larger or smaller than that represented in the illustrations.

A younger nectophore is shown in Figure 6. At that stage the thrust block was relatively small and the ascending mantle canal extended to about half its height. All the ridges were well-defined and as with most other *Bargmannia* species, except *B. stenotes* **sp. nov.**, the upper and lower laterals curved round to join together. The meso-lateral ridges ran from their proximal junctions with the upper and lower ridges obliquely down to end below the ostium. One characteristic feature was that the lower lateral ridges did not unite, distally, with the meso-lateral ridges, but petered out a short distance from them. At this stage the upper lateral ridges ran down the nectophore in parallel and very close to each other. Shortly above the ostium they clearly divided into inner and outer branches. The inner ones continued directly to the ostium, while the outer ones ran obliquely outwards for a short distance before petering out.



FIGURE 5. In situ photograph of Bargmannia profunda sp. nov. Scale unknown.

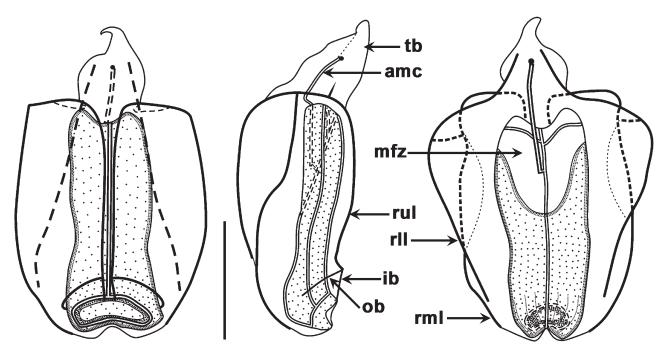


FIGURE 6. Young nectophore of *Bargmannia profunda* **sp. nov.** Upper (left), lateral (centre) and lower (right) views. See Figure 1 for list of annotations. Scale bar 5 mm.

In its preserved state the nectosac was quite narrow and approximately cylindrical. The ostial opening was broad. The long ascending mantle canal gave rise to a very short pedicular canal that in turn branched off just the upper and lower radial canals on the nectosac. The lateral canals arose, slightly asymmetrically, from the upper canal close to the apex of the nectosac. They ran obliquely out to the lateral margins of the nectosac and then straight down to the ostial ring canal. As noted above, because of damage to the lining of the nectosac it was difficult to assess the exact extent of the muscle-free zone or the position of the ostial ring canal. The ostial opening was deflected slightly toward the upper side of the nectophore, but this was almost certainly a preservation artefact. There was no mouthplate.

As the nectophores matured the main change was in the size of the thrust block (Figure 7). It became roughly triangular in shape coming to a rounded point proximally, without forming a digitate process. The ascending mantle canal extended to about half the length of the thrust block and typically ended in a small swelling inflected into the mesogloea. The lower lateral ridges extended to approximately the same level before petering out. Distally these ridges still did not unite with the meso-lateral ridges. At the junction between all three main ridges there was a thick-

ening that extended proximally for a short distance. Shortly above the ostium the upper lateral ridges branched, the inner branch running distally to the ostium, and the outer pair obliquely outwards for a short distance.

The ostial opening was wide, accentuated by the absence of the lining to the nectosac, and tended to be inflected slightly toward the upper side. The nectosac remained cylindrical in shape, and was only slightly emarginated on its proximal side. It was difficult to gauge the extent of the muscle-free zone, but it was clear that it extended slightly onto the upper side of the nectosac, proximally. The lateral radial canals arose, slightly asymmetrically, from the upper canal at a notable distance from the insertion point of the short pedicular canal.

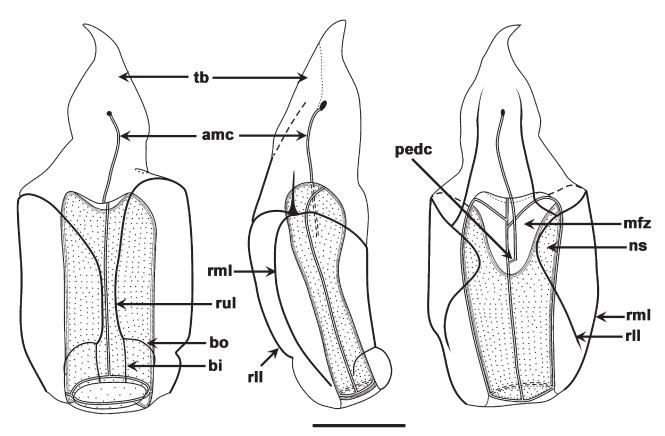


FIGURE 7. Mature nectophore of *Bargmannia profunda* **sp. nov.** Upper (left), lateral (centre) and lower (right) views. Proximal at top. See Figure 1 for list of annotations. Scale bar 5 mm.

Remarks. The arrangement of the ridges, and particularly the fact that the lower lateral ridge did not join, distally, with the meso-lateral one suggests a similarity with that of the smaller nectophores of *Bargmannia amoena*. Pugh (1999) noted that the nectophores of *B. amoena* could be split into three size categories, which probably reflected the state of sexual maturity of the colony. Nectophores of the middle range are similar in size to those of *B. profunda* sp. nov., and both had a similar ratio of overall length to nectosac length. Nonetheless, there is one feature that clearly distinguishes the two species and that is the presence of a distinct mouth-plate on the nectophores of *B. amoena*, while for *B. profunda* sp. nov. it was totally absent. This alone would seem to warrant the establishment of a new species. In comparison with the specimens of *B. amoena* also caught in the same vicinity the nectophores of *B. profunda* sp. nov. were more flaccid, in their preserved state, and the lining of the nectosac had a tendency to detach itself. Finally, the photograph of the *in situ* specimen (Figure 5) showed no sign of any pigmentation, which would be very unusual if it were *B. amoena* as colonies of that species have bright orange-red gastrozooids and the whole stem is of the same colour, as are the radial canals on the nectosac of the nectophores. Indeed the nectosac itself is usually suffused with a pale orange coloration.

Distribution. Known only from a single specimen collected off California, U.S.A at a depth of 3323 m. However, an *in situ* video frame grab of a *Bargmannia* colony (Figure 8) seen but not collected was taken during *Tiburon* Dive 853, on 7th June 2005, position 37°06.67'N, 123°57.98'W, and at the very similar depth of 3242 m (Figure 8) appeared to be very similar to the type specimen of *Bargmannia profunda* sp nov, but as it was not collected its identity remains uncertain.

Etymology. The name is derived from the Latin *profundus*, meaning deep and reflecting the great depth at which the specimen was collected.



FIGURE 8. In situ frame grab of specimen from Tiburon Dive 853.

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