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A new species of *Microeledone* from Galápagos Islands and an amended diagnosis of the Megaleledonidae (Octopoda: Incirrata)

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Abstract

The octopod fauna of the deep tropical Pacific Ocean remains poorly known, as is the octopod family Megaleledonidae Taki. A single female megaleledonid specimen collected at 1773 m depth near the equatorial Galápagos island of Darwin is named *Microeledone galapagensis* **sp. nov.** This small, squat, short-armed octopod has few arm suckers and gill lamellae. Its lack of a crop diverticulum, ink sac, and anal flaps suggests that it pertains to *Thaumeledone*. However, its smooth skin, which dorsally is nearly free of pigment, large rachidian tooth, and large funnel organ ally it with the monotypic *Microeledone*. Its reverse countershading and dense pigmentation on the inner dorsal mantle musculature distinguish this species from *Microeledone mangoldi* Norman, Hochberg & Boucher-Rodoni, 2004a. This species belies the definition of the Megaleledonidae as large-bodied, Southern Ocean endemics, leading us to revise the family diagnosis. The short arms carrying few suckers in this genus and *Thaumeledone* are hypothesized to relate to heterochrony, potentially increasing energy available for reproduction and contributing to niche partitioning.

Key words: *Thaumeledone*, heterochrony, Pacific Ocean, deep sea, posterior salivary gland, ink sac, skin texture

Resumen

La fauna de octópodos del Pacífico Tropical profundo permanece escasamente conocida, al igual que la familia de octópodos Megaleledonidae Taki. Un único ejemplar hembra de megaleledónido, recolectado a 1773 m de profundidad cerca de la isla ecuatorial de Darwin en Galápagos, es nombrado *Microeledone galapagensis* **sp. nov.** Este octópodo pequeño de brazos cortos posee pocas ventosas en los brazos y pocas laminillas branquiales. La ausencia de un divertículo en el buche, saco de tinta y aletas anales sugiere que pertenece a *Thaumeledone*. Sin embargo, su piel lisa, dorsalmente casi libre de pigmento, junto con un diente raquídeo grande y un embudo igualmente grande, lo vinculan con el género monotípico *Microeledone*. Su sombreado inverso y la pigmentación densa en la musculatura del manto dorsal interno distinguen a esta especie de *Microeledone mangoldi* Norman, Hochberg & Boucher-Rodoni, 2004a. Esta especie contradice la definición de los Megaleledonidae como especie de gran tamaño, endémica del Océano Austral, lo que nos lleva a revisar el diagnóstico de la familia. Se plantea la hipótesis de que los brazos cortos que portan pocas ventosas en este género y en *Thaumeledone* están relacionados con la heterocronía, lo que podría aumentar la energía disponible para la reproducción y contribuir a la partición del nicho.

Palabras Clave: *Thaumeledone*, heterocronía, Océano Pacífico, agaus profundo, glándula salival posterior, saco de tinta, textura de la piel

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Introduction

Incirrate octopods (Cephalopoda: Octopoda: Incirrata) of the deep eastern tropical Pacific Ocean remain virtually unstudied. Subsea vehicles that provide exceptional but all too rare opportunities to see these animals have, however, revealed unexpected taxa (Purser *et al*. 2016; Hartwell *et al*. 2018; Nautiluslive 2024; SOI 2024a, b). Among the most surprising of these may be small tropical octopods of the Megaleledonidae. This family was originally diagnosed as following the characters of the very large, Antarctic *Megaleledone setebos* (Robson), and more recently diagnosed as "Uniserial suckers. Large-bodied taxon endemic to the cold and deep waters of the Southern Ocean" (Amor *et al*. 2024: 8). However, this diagnosis ignores the 37°S (near Montevideo, Uruguay) locality of the 45 mm long type specimen of *Thaumeledone brevis* (Hoyle) and the collection of specimens of *Graneledone verrucosa* (A. E. Verrill) from as far north as 62°N off Iceland (Thomsen 1931) among many other Northern Hemisphere collections.

Collection of a female megaleledonid octopod from near the equatorial Galápagos Islands at 1773 m depth highlights the inadequate family diagnosis and motivates the description of this unique specimen. Given the near impossibility of securing a second specimen, we opted to use micro-computed tomography (µCT) to document its internal anatomy (Ziegler *et al*. 2021, Ziegler & Sagorny 2021). Given the singular specimen, we avoided use of stains, despite their ability to enhance visibility of tissues of similar density using µCT (Metscher 2009).

Here, we describe this deep-water specimen from near the Galápagos which shares many characters with the genus *Thaumeledone*, but lacks its papillose dorsal mantle and thin funnel organ. It is assigned to *Microeledone* as this genus appears to offer the best current option for formal placement of the present specimen. We amend the family diagnosis to emphasize morphology rather than geographic distribution. Given limited sampling in the deep sea, megaleledonids likely have a much larger geographic distribution and greater diversity than previously assumed.

Material and methods

In 2015, the E/V *Nautilu*s conducted the Galápagos Platform Cruise (NA064) over a ten-day period within the Galápagos Marine Reserve, exploring different deep-sea habitats across the archipelago (Salinas-de-León *et al*. 2020). Research was carried out in accordance with relevant guidelines and regulations of the Galápagos National Park Directorate. All experimental protocols were approved by the Galápagos National Park Directorate's animal care committee.

On 1 July 2015, Dive 1440 of the remotely operated vehicle (ROV) *Hercules* was conducted on a seamount about 25 km northwest of Isla Darwin (1°51'33.3"N 92°06'41.2"W). The ROV collected an octopod from a sedimented area with basalt outcrops at 1773 m depth using its suction sampler. On recovery of the ROV, the specimen was transferred to chilled seawater and photographed. The distal third of the right third and fourth arms was severed and preserved for molecular analysis; the whole specimen was then fixed in 4% formalin in seawater for 24 hours. It was subsequently transferred to 95% ethanol for storage and catalogued in the Marine Collection of the Charles Darwin Research Station (MCCDRS) as MCCDRS 10337. The tissue preserved for molecular analysis has since been lost.

The preserved specimen was subjected to the standard counts and measurements (Roper & Voss 1983), except Arm Sucker Counts (ASC), including those of the hectocotylus. Our counts include all suckers on the arm, not just those of the basal half. Measurements were made with electronic calipers and are reported in mm. Specimens identified as *Thaumeledone* from the Southern Ocean housed in the Marine Invertebrates collection of the National Museum of Scotland (RSMZ) and the United States National Museum (USNM) were also subjected to these counts and measurements for comparison. Because ASC can be affected by arm position and previous damage, count differences of four or fewer suckers were considered to be negligible.

These data were supplemented by those taken from literature accounts, which often overlapped with specimens seen during the museum visits. However, data from the type series and from specimens not deposited in the RSMZ reported by Allcock *et al*. (2004), from Argentine specimens of *Thaumeledone* reported by Guerrero-Kommritz (2006) and from the description of *Microeledone mangoldi* Norman, Hochberg & Bouchet-Rodoni, 2004a were vital.

To assess whether morphology differs between the Megaleledonidae and Enteroctopodidae, and thus could offer a valid family-level character, tests of the significance of differences in PC2 scores from an incirrate-wide

Principal Components Analysis (PCA) (Voight 1993a) and depth between species now assigned to each of the above families were conducted with a Mann-Whitney U-test.

The description of *Microeledone mangoldi* referred to the absence of functional chromatophores, and later stated that functional chromatophores were not evident (Norman *et al*. 2004a). How chromatophore functionality was determined was not revealed—the animal had been collected and preserved eleven years before its description (Norman *et al*. 2004a). Given this precedent, we use the term pigment here to avoid implicitly assuming the existence of chromatophore organs, which would require histological study of the skin to document.

To assess the relationship of mantle length (ML) and posterior salivary gland length (PSGL) with size, those of nine specimens of *Graneledone pacifica* Voss & Pearcy from Field Museum of Natural History (FMNH) and California Academy of Sciences (CAS) collections were measured. To assess their relationship among species, those of *Microeledone galapagensis* **sp. nov.** were measured and the PSGL of *M. mangoldi* was calculated from Fig. 2a in Norman *et al*. (2004a). Measurements were transformed to logarithms (log) and plotted with that of *G. pacifica,* considered to have small glands (Voss & Pearcy 1990). An attempt was made to consider PSG area and ML, but because area is the product of two measurements, its calculation compounds the variation and error, much as does the calculation of ratios (Atchley *et al.* 1976).

For µCT scanning, the specimen was removed from ethanol storage, encased in two layers of zip-top bags, and immobilized in a cardboard tube. Scanning was performed using an NSI X25 CT scanning system (North Star Imaging Inc., Rogers, MN, USA) housed at the Field Museum XCT Laboratory (RRID:SCR_026255). The scanner is equipped with a 150-kV microfocus X-ray source with a focal spot size of 20 µm (Hamamatsu Photonics, Hamamatsu, Japan) and a L08 flat-panel detector measuring 1880 x 1496 px (Varian Medical Systems, Palo Alto, CA, USA). In the scan that covered the entire specimen, scanning parameters (Table 1) were 80 kV source voltage, 375 µA source current, no filter, 2 averages, 4,734 projections over 360°, 21.02 µm isotropic voxel size, and 58 min 33 s acquisition time (6 frames per s). The region-of-interest (ROI) scan that covered the buccal mass area had parameters (Table 1) of 65 kV source voltage, 415 µA source current, 0.13 mm Cu filter, 4 averages, 2,401 projections over 360°, 8.78 µm isotropic voxel size, and 3 hr 45 min 51 s acquisition time (3.75 frames per s). The resulting 16-bit projection images were reconstructed using the software efX-CT (North Star Imaging) and saved as 16-bit tagged image file format (TIFF) image stacks.

TABLE 1. Parameters for the two µCT scans of MCCDRS 10337.

Scan	Voxel size (µm)	kV	µA	Frames per second	Frames averaged	Filter	Projections
Whole	21.02	80	375	6	2	none	4734
Buccal mass	8.781	65	415	3.75	4	0.13mm Cu	2401

Using the software Fiji 1.54p (Schindelin *et al*. 2012), the two 16-bit TIFF image stacks obtained using µCT were transformed into 8-bit format and rotated to a transverse (whole-specimen scan) or coronal (ROI scan) orientation prior to cropping uninformative parts. Based on the whole specimen image stack, the Segmentation Editor in the software Amira 5.3.1 (Thermo Fisher Scientific Inc., Waltham, MA, USA) was used to perform manual segmentation of selected internal organs. Surface rendering of the labelled organs was done using the *SurfaceGen* module with *Constrained smoothing* activated. The resulting mesh was reduced from about 2,500,000 to 100,000 faces using the *Simplifier* function and further processed using the *Smoothing* tool. The reconstructed three-dimensional (3D) model and the original dataset were rendered in Amira and screenshots were made. In addition, virtual two-dimensional (2D) sections of both datasets were created using the Volume Viewer 2.0 plugin in Fiji.

The dataset has been deposited in Morphobank (O'Leary and Kaufman 2012) at https://www.morphobank.org/permalink/?P6022. In addition, supplementary tables 1 and 2 are available there.

Taxonomy

Class Cephalopoda

Order Octopoda

Family Megaleledonidae Taki, 1961

Amended diagnosis. Benthic octopods with one row of arm suckers, short arms, broad heads and mantles; skin often textured; rachidian teeth often lack cusps, radula may be missing other teeth; in males, non-hectocotylized arm tips unmodified; hectocotylus with distinct ligula and calamus, which is often large; hectocotylus carries 55 or fewer suckers; spermatophores long, slender.

Included genera. *Adelieledone*; *Bathypurpurata*; *Bentheledone*; *Graneledone*; *Megaleledone*; *Microeledone*; *Pareledone*; *Praealtus*; *Tetracheledone*; *Thaumeledone*; *Velodona*; *Vosseledone*.

Remarks. The Megaleledonidae ranges broadly in the World's oceans, but limited sampling continues to stymie research on the group. Of the twelve currently recognized genera in the family, only four (i.e. *Adelieledone, Graneledone*, *Pareledone* and *Thaumeledone*) contained more than one species prior to this description; *Bathypurpurata* and *Microeledone* were each known only from a single specimen. The genus *Bentheledone* must be considered unstable; one authority (Allcock *et al*. 2004) states that it contains no species, while another (Norman *et al*. 2004a) argues that it does. Only the genus *Adelieledone* was defined by a suite of what may be unique characters, including those of the beak, ligula and terminal and funnel organs. Molecular analyses, also hampered by limited taxon sampling, remain largely unable to resolve relationships within the group (*e.g*., Strugnell *et al*. 2014; Taite *et al*. 2023). As a consequence, morphological characters remain critical to estimating relationships among the Megaleledonidae.

The phrase "one row of arm suckers" versus two rows is a false dichotomy (Voight 1993b). Although the number of sucker rows is frequently a very convenient, easily perceived character state, the suckers can appear to be arranged in a zig-zag, making determining the number of rows difficult. A better determinant is the relationship of ASC to arm length (Voight 1993b).

The morphology of megaleledonids may be among the family's most distinctive features. Principal components analysis (PCA) revealed that benthic octopod morphology is linked to latitude and depth distributions (Voight 1993a). When the results are re-interpreted in light of the current classification of the Megaleledonidae and Enteroctopodidae, the mean megaleledonid PC2 score of 1.63 is significantly higher than is that of enteroctopodids with a mean of 0.976 ($P = 0.00033$; $Z = -3.593$) despite statistically identical depth distributions ($P = 0.617$; $Z = 0.500$). This indicates megaleledonids have shorter arms and broader heads and mantles.

Most megaleledonids have textured skin, although species with smooth skin are known, *e.g*., *Pareledone turqueti* (Joubin) following Allcock *et al*. (2003b). Skin texture can appear nearly invariant within species (*e.g*., *Tetracheledone spinicirrhus* Voss, *Vosseledone charrua* Palacio) or be variable, as in *G. pacifica* following Voight *et al*. (2020). All cephalopods likely have skin papillae; if not visible, their components, or remnants, may be present under the skin (Allen *et al*. 2014, Voight *et al*. 2025). Whether apparent skin texture is altered by long-term chemical preservation is unknown. Hoyle (1885) stated that *Thaumeledone brevis* had smooth skin with a number of small papillae behind the left eye. Robson (1932) noted papillae on the same specimen, as are readily seen in a photograph of the holotype (Ablett *et al*. 2019). Although Robson suggested Hoyle had been in error, potentially, the papillae had become more apparent in the intervening 47 years through dehydration in alcohol storage, as Voight (2021) documented in *G. pacifica.* However, some 60 year-old specimens assigned to *Thaumeledone* stored in USNM collections (*e.g*., USNM 817377 and 884270) have smooth skin.

The Megaleledonidae includes nearly all benthic incirrate species that deviate from the typical octopod radula of nine elements, i.e. seven teeth and two marginal plates; the typical octopod rachidian carries lateral cusps. The rachidian of *Vosseledone, Velodona,* and *Tetracheledone* lacks lateral cusps (Palacio 1978), as it does in some species of the non-megaleledonid genus *Bathypolypus* following Muus (2002). Individuals of three species of *Graneledone* are known to unpredictably lack lateral cusps on the rachidian, lack marginal plates and, in extreme cases, lack some tooth rows (Voss 1976; Voss & Pearcy 1990; Allcock *et al*. 2003b; Guerra *et al*. 2012). The radula of *Vosseledone* also lacks tooth rows (Palacio 1978). In addition to radular deviations, only in this family are dramatic differences in beak size relative to ML seen, as in *Adelieledone* (Allcock *et al*. 2003c) and *Graneledone* (Voight, 2000). The unusual radula, differences in beak size and the evolution of the buccal adductor muscle in *Graneledone* (Voight 2013) suggest that this group is experimenting with buccal mass morphology in a unique way.

Genus *Microeledone* Norman, Hochberg & Boucher-Rodoni, 2004a

Type species. *Microeledone mangoldi* by original designation.

Diagnosis (amended). Small megaleledonid octopods with smooth, unpigmented skin dorsally; skin deeply pigmented ventrally; funnel organ large; radula with broad-based, sickle- or blade- shaped rachidian tooth; no ink sac, anal flaps or crop diverticulum.

Remarks. Among the twelve characters Norman *et al*. (2004a) termed "unique suite of diagnostic characters" (p. 194) for *Microeledone* are four that now help diagnose the Megaleledonidae: one row of suckers, male arm tips not modified, hectocotylus with ligula and calamus, and deep web (which relates to their short arms see Voight 1993a).

Although we cite the funnel organ as a character state, it may have little information content. The absence of the ink sac and anal flaps is recognized to be strongly linked to habitat in octopods, and to have evolved in convergence in the group (Strugnell *et al*. 2014). Less commonly recognized is that the funnel organ is functionally linked to the ink sac; it releases mucus in conjunction with the release of ink (Derby 2014). In taxa lacking an ink sac, the funnel organ is thus likely free to vary without functional constraint. An extreme example is the octopodid *Ameloctopus litoralis* Norman which lacks an ink sac and has only a remnant funnel organ (Norman 1992). Variation in funnel organ shape among other taxa without ink sac is largely unexplored, although it has been noted in three species of *Graneledone* (Voss 1976; Voss & Pearcy 1990; Allcock *et al*. 2003a—who suggested the variation was due to preservation artefacts) and in species of *Bathypolypus* by Muus (2002).

Very large posterior salivary glands can no longer be among the diagnostic characters of the genus. The glands in *M. mangoldi* were reported to be very large, "almost as long as the buccal mass" (Norman *et al*. 2004a, p. 195) or 88.5% of buccal mass length; they were cited (Norman *et al*. 2004a, Table 3) as contributing to separating this taxon from those of *Thaumeledone* with large glands 70–80% of buccal mass length. The term "very large" is troubling, as it is most often applied when the posterior salivary glands exceed the length of the buccal mass (e.g., Norman (2001) for *Octopus micros* and *O. bulbus*; Norman *et al*. (2004b) for *Galeoctopus lateralis*); Allcock *et al.* (2003c) termed those of *Pareledone* to be "medium size … approximately equal to length of buccal mass" (p. 423). Norman *et al.* (2005) followed suit, terming the posterior salivary glands of three new species of *Scaeurgus* to be moderate in size, at 75.4, 82 and 84% of the buccal mass length, as did Gleadall *et al*. (2010) in regard to the glands of *Muusoctopus*. Following this usage, the posterior salivary glands of *M. mangoldi* and of *Thaumeledone* species at these same relative percentages of buccal mass length are better considered to be medium in size rather than very large. Below we discuss variation in this character.

Microeledone galapagensis sp. nov.

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(Fig. 1–5)

Type material. Holotype: ECUADOR: Galápagos Seamount: NW Darwin ca. 25 km northwest of Isla Darwin (1°51'33.3"N 92°06'41.2"W) at 1773 m depth. MCCDRS 10337, female, ML = 31.5 mm.

Diagnosis. With the characters of the genus; sheath covering inner dorsal mantle muscles heavily pigmented, internal organs lack pigment, except dots near mantle opening on mantle septum, rectum, and anus; posterior salivary glands medium, ca. 70% of buccal mass length; eyes large, slightly projecting.

Description. Squat: mantle width slightly less than length. Head narrower than mantle, no nuchal constriction (Fig. 1, 2C; Table 2). Mantle wall appears thin (Fig. 2B).

Eyes large, slightly projecting, not meeting at midline (Fig. 1D, 2C). Arms short, less than 1.4x ML, round in cross section; subequal, I=II>III=IV, up to 33 uniserial suckers on each (Fig. 1; Table 2). Sucker diameter roughly constant along arm, being very slightly the largest within the web, tapering rapidly near tip; no enlarged or modified suckers. Suckers tall, straight. Web sectors subequal, deep between all arms; A=B=C=D>E.

TABLE 2. Measurements (in mm) and counts of the holotype of *Microeledone galapagensis* **sp. nov.** ML = mantle length; MW = mantle width; HW = head width; ALR1/ASC = arm length right arm one/ arm sucker count of right arm one; each arm reported in the same format; SD = sucker diameter; Gill count; Web A = depth of dorsal web sector; B R/L sector B right/left etc. for each sector. PSG length = posterior salivary gland length. Funnel length, free funnel length and eye opening diameter are self-explanatory.

Depth (m)	1773
sex	F
ML	31.5
MW	28.7
HW	23.2
ALR1/ASC	40/31
ALR2/ASC	38/33
ALR3/ASC	-
ALR4/ASC	-
ALL1/ASC	43/30
ALL2/ASC	42/31
ALL3/ASC	30/33
ALL4/ASC	38/29
SD	1.7
Gill count	5+1/5
Web A	23
B R/L	24/25
C R/L	23/24
D R/L	23/23.5
E	21
PSG length	5.2
Funnel length	10.2
Free funnel length	3.8
Eye opening diameter	5.04; 4.6

Funnel (Fig. 2A, B) length 10.2 mm; free length 3.8 mm. Funnel organ: poorly defined, so large it occupies most of the inner funnel, base unclear. Two- if not four-parted; on each side, lateral limb joins medial limb broadly, lateral limb shorter than medial limb, broad with pointed tips.

Sheath over inner dorsal mantle muscles covered with dense pigment; organs not covered by pigmented sheath. Internal mantle with little pigment: several pigmented dots on mantle septum near mantle opening; two on rectum; six dots surround anus.

Five gill lamellae. Small transparent stylets present, 6 mm long, with slight bend in middle, delicate, transparent (Fig. 3B).

Esophageal crop broad, without diverticulum (Fig. 3A). Posterior salivary glands 70% of 8.5 mm long buccal mass, left 5.2 x 3.8 mm; right 6 x 4 mm (Fig. 3A). Stomach bipartite; proximal part muscular; distal part softer. Caecum one whorl, slightly orange externally, contains sediment and one or two foraminifer tests (Fig. 3A). Pancreas: patch of grey material superficial on digestive gland where broad ducts from cecum enter. Intestine thin, apparently empty, exits caecum, makes a hairpin turn, then descends with a slight taper to anus; closely adherent to ovary and hepatopancreas. No ink sac. No anal flaps.

Ovary occupies considerable space in the mantle cavity (Fig 2B, D; Fig. 4A). Ovarian capsule more membranous than tough, not taut against its eggs. Thirteen ovarian eggs *in situ*, up to 11 x 6.5 mm; seven folds at non-stem end (Fig. 4B). Distal oviducts conspicuously retracted (Fig. 4A), small muscular star-shape opening near center; contraction may generate their comparatively massive girth, equal to 5 mm diameter oviductal gland (Fig. 4A). Oviductal glands 2.3 mm long, greenish; sections not well-defined externally, visible using µCT (Fig. 4C). Proximal oviducts uncontracted, slender, 7.5 mm long, connect individually to enlarged (11.4 x 20.0 mm), extremely stretched ovary. Despite evidence of reproductive maturity, no unequivocal signs of senescence, such as notably reduced digestive gland, or abundant connective tissue and blood vessels in mantle, present.

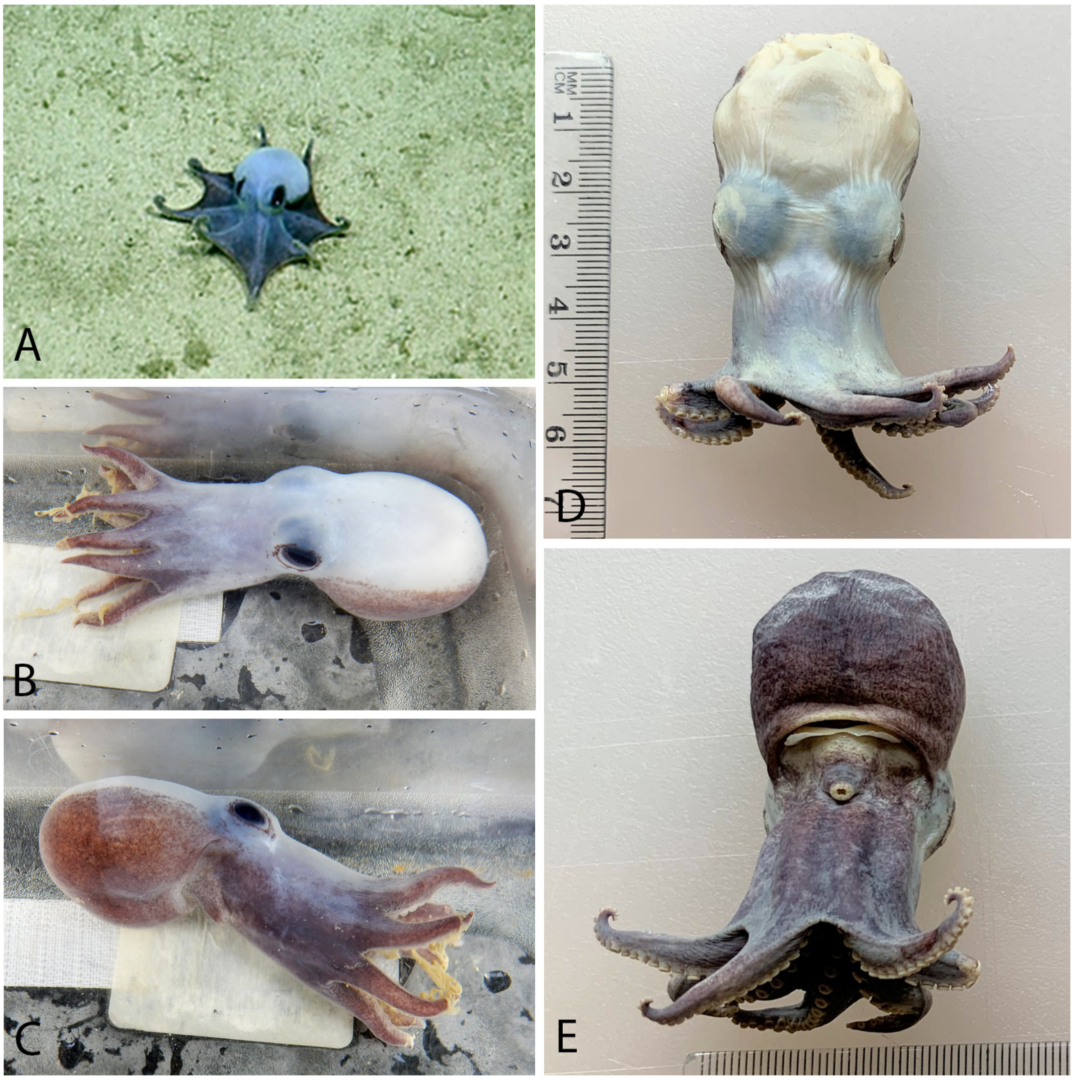

FIGURE 1. Photos of *Microeledone galapagensis* **sp. nov.** *in situ* (a); on recovery dorsal (b) and ventral (c) (photos by the Science Party of the NA064 cruise); in preservation dorsal (d) and ventral (e) views of entire animal.

Beaks visualized using µCT (Fig. 5 C, D, E) with large rostrum. Buccal mass with standard configuration, radula rests on radular bolsters (Fig. 5A), foraminifera tests scattered in food groove (Fig. 5A). Rachidian tooth with broad base with narrow central cusp (Fig. 5B), lateral teeth not visible perhaps due to small size or flattened shape (Fig. 5B).

Strong reverse counter-shading (Fig. 1). Externally, pigment nearly absent from dorsal mantle; 5–6 scattered dots of pigment between eyes and 50–60 small pigmented dots clustered near posterior mantle tip. Pigment encircles the eye, but noticeably reduced dorsally (Fig. 1B); dorsal head white. Pigment near lateral mid-mantle reminiscent of spider webs, becoming dense on ventral mantle (Fig. 1B, C). Ventral to mid-mantle, pigmentation dramatically increases, as on third and fourth arms and aboral web sectors D and E (Fig. 1C, E). Oral surface of arms and web uniform deep purple with an overlying white layer that may be mucus; oral surface of suckers colorless. Distal half of aboral arms I and II with scattered pigment; color on proximal arms largely restricted to web margin (Fig. 1D). Distal two-thirds of aboral arm III with scattered pigmentation. Arms IV pigmented (Fig. 1E). Ventral mantle maroon, arms and web more purple in preservation, although more maroon distally when fresh (Fig. 1C, D).

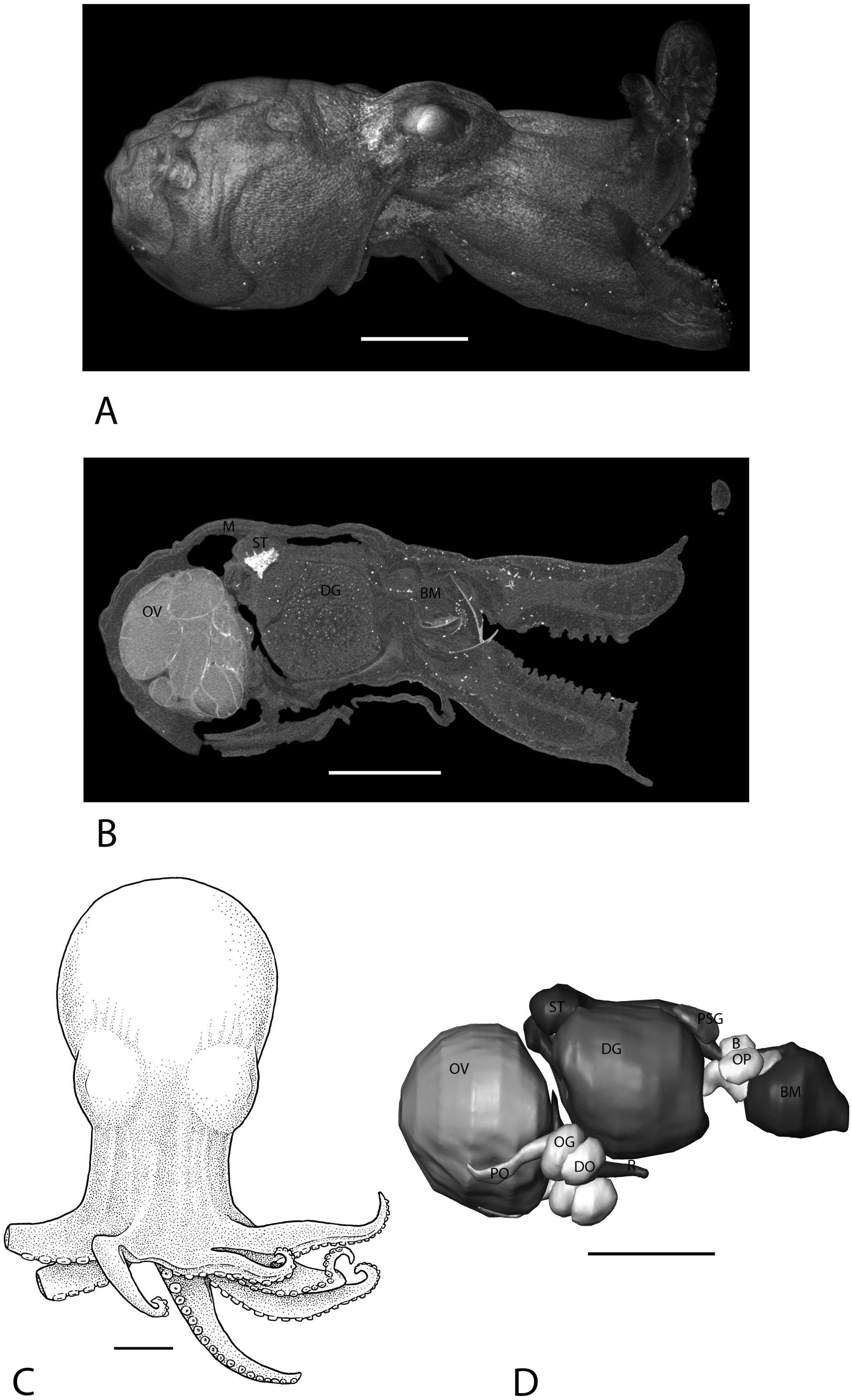

FIGURE 2. (a) μCT scan of outside of specimen; (b) μCT virtual cross section of specimen, including the mantle (M), digestive gland (DG), ovary (OV), stomach (ST), and buccal mass (BM) arms to the right; (c) drawing of dorsal view of the holotype, (d) μCT scan of lateral view of the digestive gland (DG), ovary (OV), proximal oviduct (PO), oviductal gland (OG), stomach (ST), rectum (R), brain (B), optic gland (OP) and buccal mass (BM) of specimen, arms to the right. Scale bars a & b 9.98 mm; c and d 10 mm.

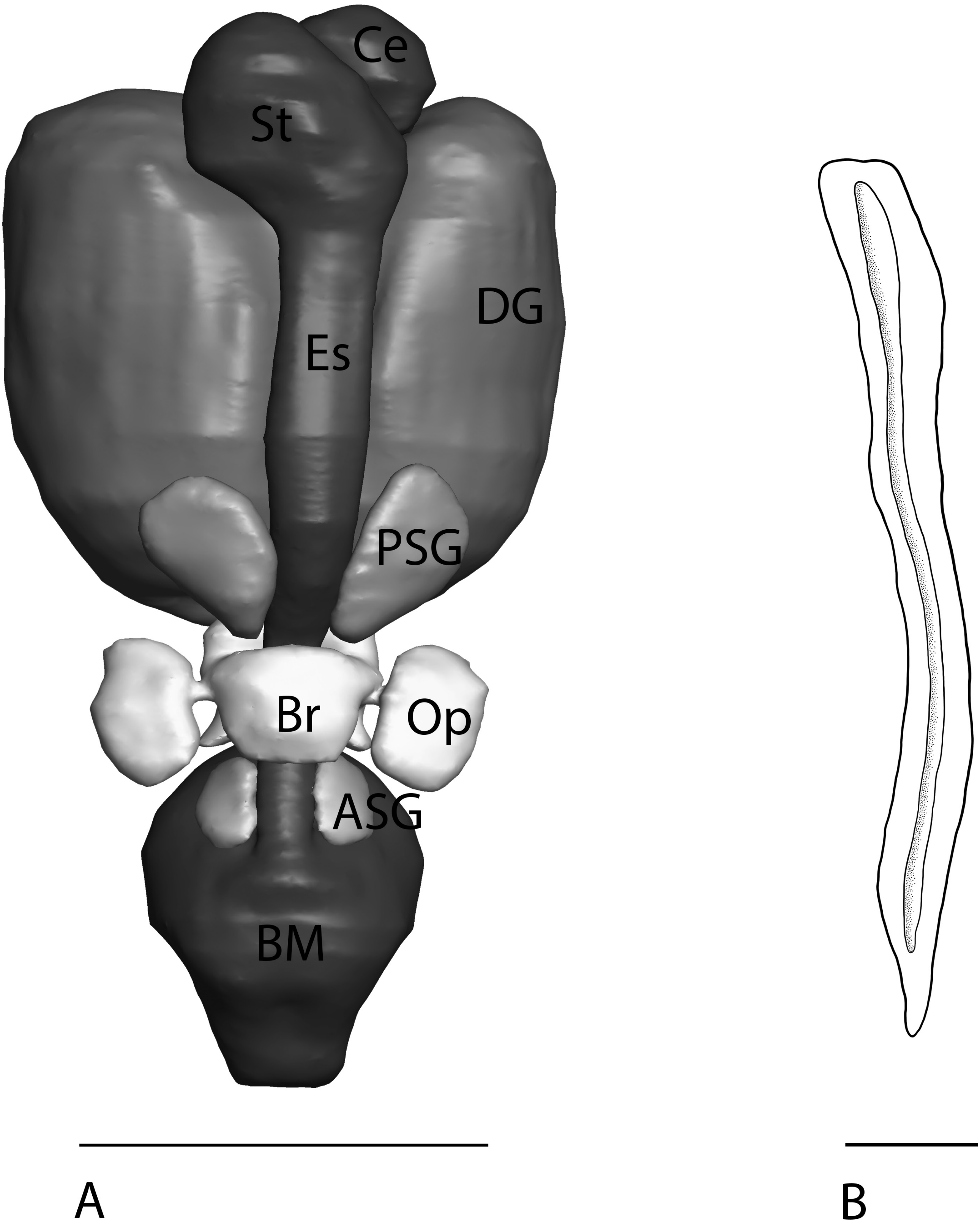

FIGURE 3. (a) µCT image of dorsal mantle organs including buccal mass (BM), anterior salivary glands (ASG), brain (Br), optic glands (Op) posterior salivary glands (PSG), esophagus (Es), digestive gland (DG), stomach (St), and cecum (CE); (b) Stylet. Scale bars a 10.01 mm; b 1.0 mm.

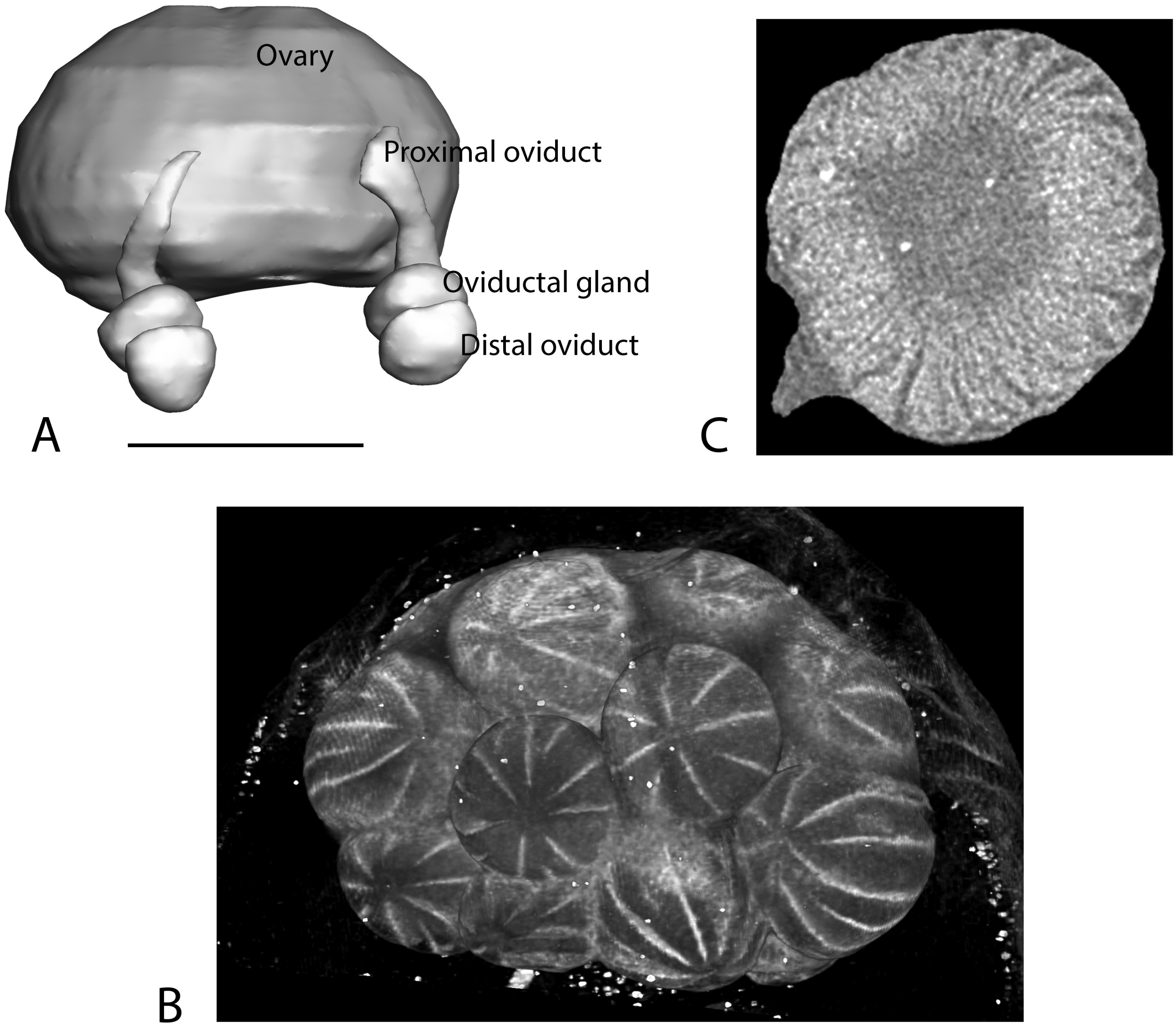

FIGURE 4. (a) µCT image of ventral ovary with ducts labeled scale bar 10.01mm; (b) µCT image of dorsal ovarian eggs; (c) µCT cross section of oviductal gland (5 mm in diameter).

No detectable papillae on skin, either in photos from life or preserved specimen (Fig. 1). No supraocular cirri. After extended storage in 95% ethanol, subtle, short longitudinal ridges apparent on the mantle (Fig. 1D, Fig. 2C). Skin wrinkled, taut around eyes, suggesting desiccation (compare Fig. 1B, 1D); if gelatinous layer had been present in skin of mantle and arms, no trace remains.

Distribution. In addition to the type locality at 1°51'33.3"N, 92°06'41.2"W (1773 m depth), two additional octopods that appear conspecific with the holotype were observed but not collected during the same ROV dive (H1440) at depths between 1770–1800 m, approximately 1–2 km from the collection site. An additional individual, morphologically consistent with the species, was also recorded at 2006 m depth during Dive H1436 on an adjacent seamount located about 60 km southeast of the type locality (1°39'64"N, 91°40'51"W). All individuals were observed resting on sandy substrate.

Derivation. Named in honor of the islands close to the collection locality.

Remarks. The smooth skin and large funnel organ of the present specimen prevent it from being assigned to *Thaumeledone* as defined by Norman *et al*. (2004a), despite the shared squat morphology and relatively low arm sucker and gill lamellae counts. The lack of detectable skin texture is exceptional. As noted above, the presence of skin papillae may be a common feature among cephalopods and remnants of papillae may exist undetectable in the skin (Allen *et al*. 2014; Voight *et al.* 2025). However, the wrinkled, possibly desiccated skin posterior to the eye in

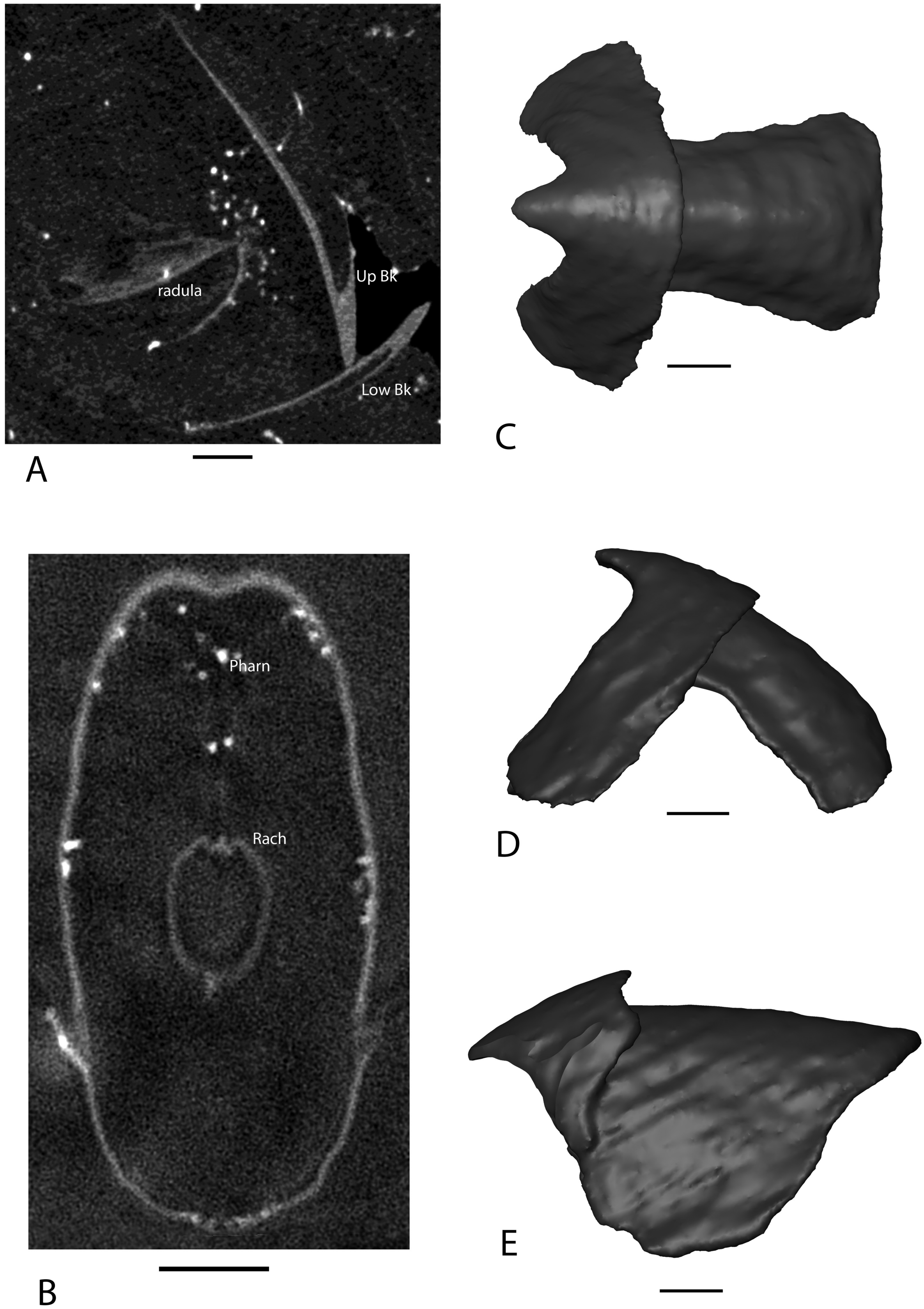

FIGURE 5. (a) µCT longitudinal view through the buccal mass, showing rostrum of the upper beak (UpBk) and lower beak (Low BK), and radula. Bright white dots are likely foraminifera tests; (b) Transverse µCT image of the buccal mass, showing the beaks (outer lightest colored line) encircling the buccal cavity with radular bolsters defining the pharnyx and the rachidian (Rach) visible as a small, light colored inverted "T"; (c) µCT scan of ventral lower beak; (d) µCT scan of lateral lower beak; (e) µCT scan of lateral upper beak. All scale bars 1.0 mm.

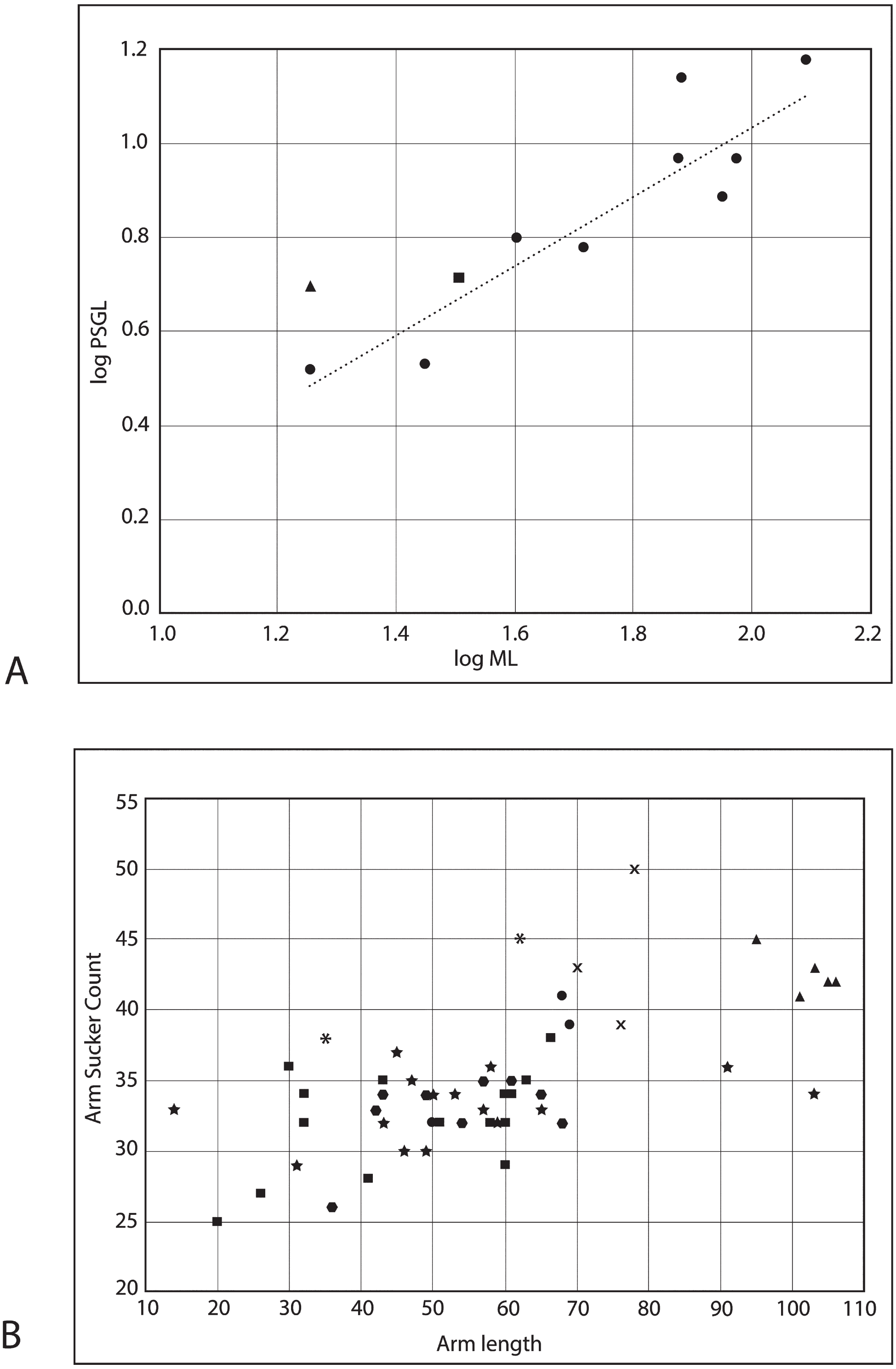

FIGURE 6. (a) Plot of log mantle length (ML) versus log posterior salivary gland length (PSGL) for *Graneledone pacifica* (circles) with the regression line indicated, *Microeledone mangoldi* (triangle) and *Microeledone galapagensis* **sp. nov.** (square). Raw data in Table S1. (b) Plot of maximum arm length versus highest arm sucker count. Specimens assigned to *Thaumeledone brevis* (Hoyle) collected between 59–61.6°S 49.14–61.1°W at 785–3,854 m depth are represented by squares, In addition, those assigned to *T. brevis* from the Ross Sea (74.1°S 175.025°W, from 1,800 to 3,270 m depth, USNM 817372, 817374, 817375) are represented by X's, those from the South Atlantic Ocean (62.15°S 40.642°W, 3,267 m depth, USNM 884270) by asterisks and from the Argentine Sea (46°55'S 60°W, from 400 to 1,000 m depth) by circles. Counts from *Thaumeledone rotunda* Hoyle are represented by triangles, *Thaumeledone gunteri* Robson represented by stars and *Thaumeledone peninsulae* Allcock, Collins, Piatkowski & Vecchione represented by hexagons. Two squares in the lower left of the plot with 25 and 27 suckers are the type specimens of *T. brevis* from off Uruguay (Allcock *et al*. 2004). Table S2 reports locality information.

this preserved specimen (Fig. 1D), could reasonably be expected to reveal any papillae. Until new specimens and more information become available that refute this action, we consider this species to belong to *Microeledone* as it appears to offer the best current option for formal placement of the present specimen.

This new species shares with *M. mangoldi* smooth skin, large funnel organ, reproductive maturity at a small size (given that female octopods mature at larger sizes than males), mantle areas lacking pigment, a large, broad-based rachidian, and similar arm sucker and gill lamellae counts (discussed below). The species can be distinguished primarily by the distribution of color inside the mantle: the new species has color on the inner lining of the dorsal mantle muscles, *M. mangoldi* has color on sheaths over the organs themselves (Norman *et al*. 2004a). If this species shares a common ancestor with *M. mangoldi*, these differences may be convergent adaptations to concealing ingested bioluminescent prey, suggesting they took separate paths into the deep sea. Posterior salivary gland size, being smaller in this species than in *M. mangoldi* (Fig. 6A), based on a single specimen of each species, and the greater extent of reverse countershading in the present species contribute to their separation.

The radula in the present species is very difficult to see using µCT. However the broad base of the rachidian is clearly visible (Fig. 5B) and similar to that of *M. mangoldi* (Norman *et al.* 2004a), to those of *Thaumeledone* spp. illustrated by Allcock *et al.* (2004) and to that of *Vosseledone charru* shown by Palacio (1977). Although Palacio (1977) stated the rachidian had a narrow base, it appears much broader than the tooth itself (Palacio 1977 Fig. 3). In that taxon, the lateral teeth appear to be flat, as do those of *M. mangoldi* and *T. gunteri* shown by Norman *et al.* (2004a). These are not inconsistent with that of the present species.

Results and Discussion

Use of entirely non-invasive (*i.e.*, no stain used) µCT scanning of a formalin-fixed and ethanol-preserved museum specimen provided sufficient soft part contrast to extract characters for a full octopod species description. This is a significant methodological advance valuable in documenting such rare specimens, and revealing characters such as the interior structure of the oviductal gland (Fig. 4C) and the contents of the stomach (Fig. 2B). The foraminifera were likely ingested with prey and retained, as is common with indigestible fragments in octopods (Sykes *et al.* 2020). The proximal extremities of the beak were not clearly shown using µCT, as they often lack the tanning typical of the central parts of the beak.

A character well-documented by µCT-scanning is posterior salivary gland length (PSGL) (Fig. 3A, Table S1). It contributes to separating the present species from *Microeledone mangoldi*. Our investigation of intraspecific variation in posterior salivary gland size found log PSGL correlates with log ML in nine specimens of *Graneledone pacifica* ($r^2 = 0.836$; Fig. 6A; Table S1). Despite the predictable increase in gland length with increasing ML (i.e. growth), considerable variation exists, much more than in comparisons of the uniformly muscular arms and mantle of shallow-water octopods (Voight 1991). Two specimens of *G. pacifica* with ML's of 75 and 76 mm have posterior salivary glands 9.3 and 13.8 mm long, respectively; the specimen collected over 1300 m deeper has the longer glands (Fig. 6A, Table S1). The unknown extent of intraspecific variation in PSGL (apparent among only nine specimens of *G. pacifica,* Fig. 6A), the known impact of habitat depth on gland size in *Thaumeledone* (Voss 1988; Allcock *et al*. 2004), and the potential influence of prey type on gland size (Voss 1988) question heavy reliance on this character.

Although helpful in some octopods, arm sucker count (ASC) among species of *Thaumeledone* and *Microeledone* is very limited (Fig. 6B). Among most specimens assigned to three species of *Thaumeledone* and the single specimens of *M. galapagensis* **sp. nov.** and *M. mangoldi,* ASC ranges from 32 to 37, regardless of arm length (Fig. 6B; Table S2). Two unidentified specimens of *Thaumeledone* (RSMZ 2008090.15) have 16.5 and 18 mm long arms that carry 33 and 34 suckers, as do the 14 mm long arms of *T. gunteri* Robson (USNM 817404); a conspecific specimen (RSMZ 1999275) with arms 103 mm long carries only one more sucker (Fig. 6B). *Thaumeledone rotunda* (Hoyle) is unusual in having up to 45 suckers in contrast to the 36 on equally long arms of *T. gunteri*. Few specimens have fewer than 30 suckers per arm, notably the small type specimens of *T. brevis* from off Montevideo (Fig. 6B). Whether the seemingly anomalous ASC in specimens from geographically distinct areas (Fig. 6B) reveals genetically isolated populations is to be determined. These data, however, support the hypothesis of Guerrero-Kommritz (2006) that greater interspecific diversity exists in megaleledonids than has been acknowledged and merits additional study.

Recruitment of the full sucker complement at quite small sizes (Fig. 6B) may indicate the heterochronic process paedomorphosis, resulting in animals being morphologically juvenile, but sexually mature. Whether the mechanism is progenesis, i.e., acceleration of the onset of sexual maturation compared to the rest of development, or neoteny, i. e., the slowing of somatic development compared to sexual maturation, cannot be determined without knowledge of the ancestral characters. Paedomorphosis may contribute to increasing energy available for reproduction and to niche differentiation among sympatric amphibians (leJeune *et al*. 2020), as it might among sympatric octopods.

Uncertain reliability of the above characters and, in the case of Arm Sucker Count, limited variation, suggest that the absence of pigment from the dorsal mantle shown in situ, in the fresh specimen and in preservation (Fig. 1) is prominent among features defining the genus. Although species of *Muusoctopus* can show seemingly identical reverse counter-shading in life, when relatively fresh, their light-colored dorsum can darken as it gradually does in preservation to obscure the counter-shading (JRV, unpub. obs.). Species of *Microeledone* do neither. Support for the information content of octopod color and skin texture lies in Voss' (1950) citation of these features in describing *Octopus burryi* Voss; over 50 years later Huffard & Hochberg (2003) cited the same features in their resurrection of the genus name *Amphioctopus*.

Although one could argue that a mature male is needed for a species description, the ligula and/or calamus in this taxon will likely be exceptionally large, similar to the three-dimensional calamus with a muscular and concave ligula that Allcock *et al*. (2004: Plate 5 inset) illustrate in *Thaumeledone*. Thorson's rule predicts octopods living in cold temperatures will produce large spermatophores (Ibáñez *et al*. 2018). Octopods with short arms, and thus even shorter hectocotyli, may have evolved unusually large male intromittent organs, notably the calamus in *Thaumeledone* and, in convergence, the large ligula of *Bathypolypus,* to compensate.

Documented character variation in a series of conspecific specimens from a range of depths, and molecular analyses are needed to increase our knowledge of this still enigmatic family. In the case of the megaleledonids, their natural history and phylogeny are likely more complex than has previously been assumed.

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