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A new Western North Atlantic Ocean kitefin shark (Squaliformes: Dalatiidae) from the Gulf of Mexico

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Abstract

A new species of kitefin shark (Squaliformes; Dalatiidae) is described from the Gulf of Mexico (Western North Atlantic Ocean) based on five diagnostic features not seen on the only other known *Mollisquama* specimen, the holotype of *Mollisquama parini* Dolganov which was captured in the Eastern South Pacific Ocean. The new species, *Mollisquama mississippiensis* **sp. nov.**, is distinguished from its congener by a putative pit organ located ventrally just posterior of the lower jaw margin center, photophores irregularly distributed along many areas of the body, 16 distinct ventral-abdominal photophore aggregations, and two differences associated with the dentition. Other potential distinguishing features are 10 fewer vertebrae than *Mollisquama parini* and six morphometric proportional differences that exceeded +/- 20% from the holotype.

Key words: *Mollisquama mississippiensis* **sp. nov.**, bioluminescent shark, putative pit organ, synchrotron scans

Introduction

Kitefin sharks in the family Dalatiidae (Squaliformes) comprise seven genera (*Dalatias*, *Euprotomicroides*, *Euprotomicrus*, *Heteroscymnoides*, *Isistius*, *Mollisquama*, and *Squaliolus*) of which five are monotypic (*Isistius* and *Squaliolus* contain two species each). They are distinguished from other squaliform sharks by their robust lower jaws, degree of dignathic heterodonty, dorsal fins without spines (except *Squaliolus*), and the lack of an anal fin (Bigelow & Schroeder 1948). Dalatiids are distributed world-wide in most temperate, subtropical and tropical marine waters and descriptions of their life histories, distributional ranges and behavior are often based on few museum specimens and a paucity of reliable observations. Not much is known about dalatiid life histories, but it is known that they are viviparous (Gadig & Gomes 2002) with embryos nourished *in utero* by a yolk sac and birth of fully-formed young that are miniatures of the adults. Some species are known to be luminescent (Claes *et al*. 2014), a feature that may aid in attracting prey or eluding predators. Additionally, counter-illumination by photophores on the ventral surface may facilitate predatory behavior and render them practically invisible from below. Dalatiid sharks of the genus *Isistius* (cookiecutter sharks) employ a unique feeding behavior, the details of which are not fully understood. They excise an oval flesh plug (Strasburg 1963; Shirai & Nakaya 1992) from a variety of prey including marine mammals, sharks, tunas, billfishes, squids, and infrequently, humans (Jones 1971; Dwyer & Visser 2011; Gallo-Reynoso *et al*. 2005; Papastamatiou *et al*. 2010; Hoyos-Padilla *et al*. 2013; Honebrink *et al*. 2011; Ribéreau-Gayon *et al*. 2017; Ribéreau-Gayon *et al*. 2018; Grace *et al*. 2018). Here we describe a new species of dalatiid shark of the genus *Mollisquama* based on a single specimen captured from the Gulf of Mexico (Figs. 1A, B; illustrations previously from Grace *et al*. 2015). Phylogenetic analysis of DNA sequence data (mitochondrial NADH2 gene) places *Mollisquama* in Dalatiidae as sister to *Isistius* (Grace *et al*. 2015; Denton *et al*. 2018).

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Methods

Photographs, high resolution CT scans, and x-ray synchrotron scans (composite layer synchrotron scans of 6.24 µm voxel layers) were used to examine tooth morphology (Fig. 2) and establish tooth counts.Vertebral counts were made from radiographs and high-resolution CT scans (Fig. 3). The description of the putative pit organ and associated dermal denticles was based on a physical examination made with the aid of a computer-linked digital dissecting scope that was also used for photographs (Fig. 4A). SEM micrographs were used to examine dermal denticles from the right side dorsolateral area below the first dorsal fin (Fig. 4B; previously from Grace *et al*. 2015). Internal organs were examined from synchrotron scans (Figs. 5, 6) or histological sectioning. Discussions about distinguishing features are confined to the holotype (Dolganov 1984) and other dalatiids, with the exception of the discussion about photophores that includes comparisons with Etmoperidae, the only other shark family with photophores that have been described in detail based on histology. Photophore occurrence has been reported for *Zameus* sp. (Somniosidae; Straube *et al*. 2015); however, a description based on histology is not yet available for a comparative discussion.

Mollisquama mississippiensis **sp. nov.**

Figures 1, 2, 3, 4, 5, 6; Table 1, 2
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Mollisquama sp. (Grace *et al*. 2015)
Mollisquama aff. *parini* Dolganov 1984 (Del Moral-Flores *et al*. 2015)
Mollisquama parini Dolganov 1984 (Weigmann 2016)
Mollisquama sp. (Denton *et al*. 2018)
Mollisquama parini Dolganov 1984 (de Figueiredo Petean & de Carvalho 2018)

Holotype: —TU 203676, central Gulf of Mexico, NOAA Ship *PISCES* survey 7620101001, station 053, 4 February 2010, 142.0 mm total length, 14.6 g, immature male.

Diagnosis. Differs from the only other described species of *Mollisquama*, *M. parini* (Zoological Institute, St. Petersburg, Russia, ZIL-45988), in having a putative pit organ centrally placed just posterior to the lower jaw margin, photophores irregularly distributed along many areas of the body, a series of 16 ventral-abdominal photophore aggregations, upper teeth without a labial-surface ridge (*M. parini* has a labial-surface ridge), and lower teeth with a weak or absent basal sulcus (*M. parini* has a deep basal sulcus). The distinguishing external features the pit organ and photophore aggregations were clearly discernable when the new species was captured (Grace *et al*. 2015) and after preservation. These features were not reported as present on *M. parini*.

Description. *Gross Morphology*. Resembles *M. parini* in general shape, fin placement, fin shapes, and pectoral-area pocket glands (distinguishes *Mollisquama* spp. from all other elasmobranchs). Total vertebrae 73; 37 monospondylous precaudal centra and 36 diplospondylous caudal centra (Fig. 3). A putative pit organ 2.5 mm posterior to the lower jaw margin center with a radiating arrangement of bordering dermal denticles (five radiating dermal denticles in first proximal row, Fig. 4A); rounded center protuberance (0.5 mm diameter) equal in height to bordering denticles and ringed with approximately 20 low nodules, two half-circle wedges at center separated by a groove. Along the ventral-abdominal surface a series of 16 photophore aggregations extend from approximately 5.0 mm posterior of lower jaw to anterior of pelvic fin origin (Fig. 1B), anterior to posterior numbering 2, (followed by the healed vitelline scar), 2, 2, 3, 2, 1, 1, 1, 1, 1; aggregations completely covered by dermal denticles oriented on an rostral-caudal axis, at aggregation centers numerous dark clusters of photophores surrounded by a lighter-grey area with fewer photophores; additional photophores irregularly distributed along many other areas of the body.

Cylindrical body tapers towards a slender caudal peduncle, nearly circular in cross section, followed by a bi-lobed homocercal caudal fin with rounded apexes. Wide head considerably deeper than the rest of the body with a broadly-rounded bulbuous snout (in profile) with a subterminal mouth. Head width greatest just posterior to spiracles. Oral furrows extend past mouth corners to below spiracles. Orbits elliptical and positioned level with nostrils and anterior to and just ventral of spiracles. Five small gill slits surrounded by light cream-colored distinct bar, posterior gill slit over pectoral fin origin. Distinct, cream-colored blotch at dorsal and ventral-posterior margin of pectoral fin base. Pocket gland opening above pectoral fin base and approximately half the length of the pectoral fin base, opening surrounded by 14 shallow dermal folds with lighter blue-grey corners, gland interior lined with numerous dark villi. Two low dorsal fins positioned above the pelvic fin. Spines absent on all fins and no anal fin, caudal keels or precaudal pits. Dermal denticles spade-shaped with type-I scale morphology (Reif 1985), more prevalent overlapping at fin bases, covering the body except for posterior margins of fin tips, relatively translucent with four rows of ectodermal pits and a darker pedicle center (Fig. 4B). Body color coal grey with brown undertones, slightly counter-shaded (dark dorsally and lighter ventrally). Fins dark with distinctly lighter ceratotrichia fringes along posterior margins (<2.0 mm length). Lateral line darker than background body color. Lighter pigmentation around and within mouth. Additional diagnosis of features and morphometric values are found in Grace *et al*. (2015) and Denton *et al*. (2018), and specimen photographs taken just after capture are found in Grace *et al*. (2015).

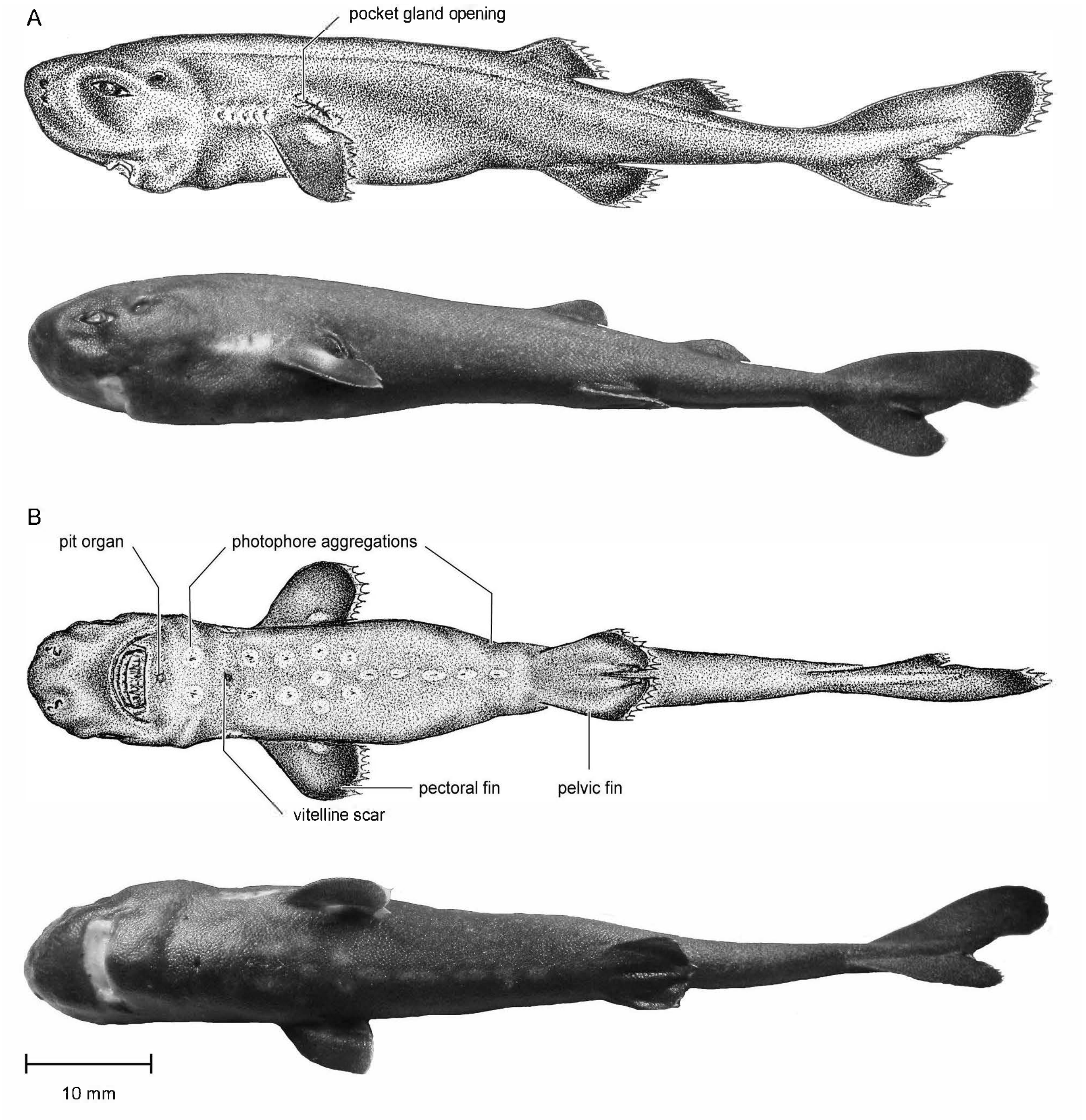

FIGURE 1. *Mollisquama mississippiensis* **sp. nov.**, TU 203676 illustrated to scale in (A) lateral and (B) ventral view.

Dentition. Dignathic heterodonty with upper teeth narrow and conical without a labial-surface ridge and lower teeth broad and bladelike (Fig. 2). Upper and lower teeth decrease in size toward mouth corners. Symphyseal teeth present in both upper and lower jaws; lower jaw symphyseal tooth with flanking shoulders below the cusp that overlaps adjacent teeth. Upper teeth with a broad-forked root and cusps slightly curved posteriorly. For lower teeth the root height is approximately 50% of the total tooth height and most cusp tips curve toward jaw corners. For lower teeth the basal sulcus is absent or weakly present (Denton *et al*. 2018). Dental formula 10-1-10/15-1-15 (Denton *et al*. 2018).

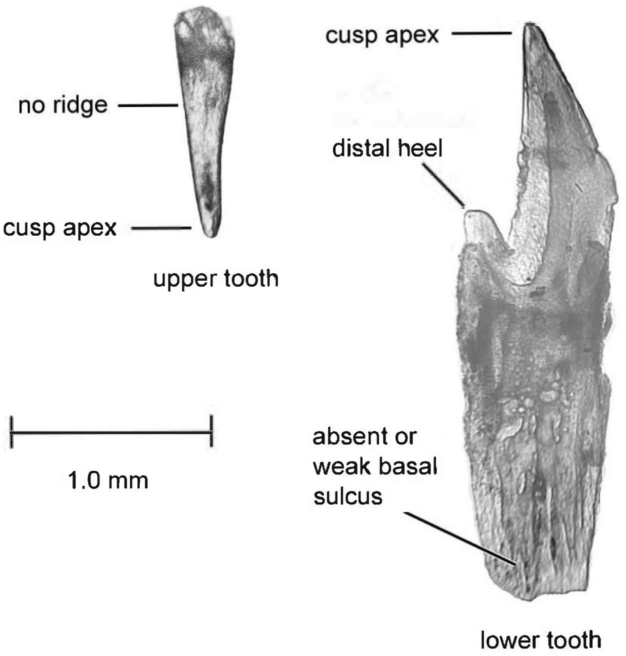

FIGURE 2. *Mollisquama mississippiensis* **sp. nov**., upper tooth lateral view (tooth #4 right); lower tooth labial-surface view (tooth #4 right).

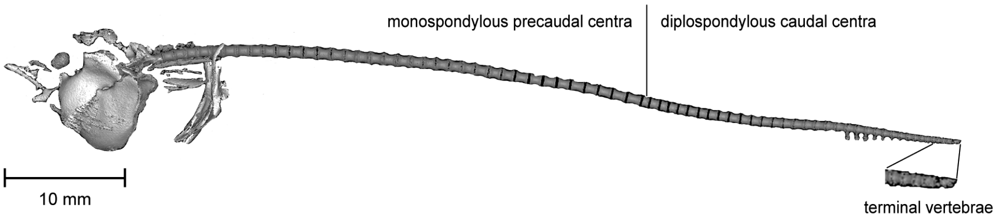

FIGURE 3. *Mollisquama mississippiensis* **sp. nov.** CT scan of vertebral column (http://sharksrays.org/).

Habitat. The new species was captured with a midwater trawl (07:01 U.S. Central Standard Time, 4 February 2010, 2 h trawling effort) during a cetacean research project to assess predator/prey trophodynamics for sperm whales (*Physeter macrocephalus*) of the Gulf of Mexico (NOAA Ship PISCES survey PC10-01; location 26 18.55ºN/-087 25.75ºW, Fig. 7). Trawl fishing depths were from 5 m of surface to a maximum trawl fishing depth of 580 m over 3,038 m bottom depth; the sea bottom was a relatively flat abyssal plain without significant bathymetric features. Environmental sampling was conducted within 10 nautical miles of the trawl location. Surface/maximum trawling depth environmental data was; temperature 21.5ºC/7.2ºC, oxygen saturation 6.6 mg/l/ 4.0 mg/l, and salinity 36.5 psu/34.9 psu. Other fauna captured included 44 species identified to lowest taxon (3.3 kg total catch weight, 731 specimens); 29 finfish taxa, 15 invertebrate taxa. Grace *et al*. 2015 includes a comparative discussion of the considerably-different collection locations of *Mollisquama* spp. (e.g., *M. mississippiensis* **sp. nov.** captured above an abyssal plain 3,038 m depth influenced by the relatively warm Gulf Stream; *M. parini* captured above an extensive seamount ridge 330 m depth that is influenced by the relatively cold sub-Antarctic Humboldt Current).

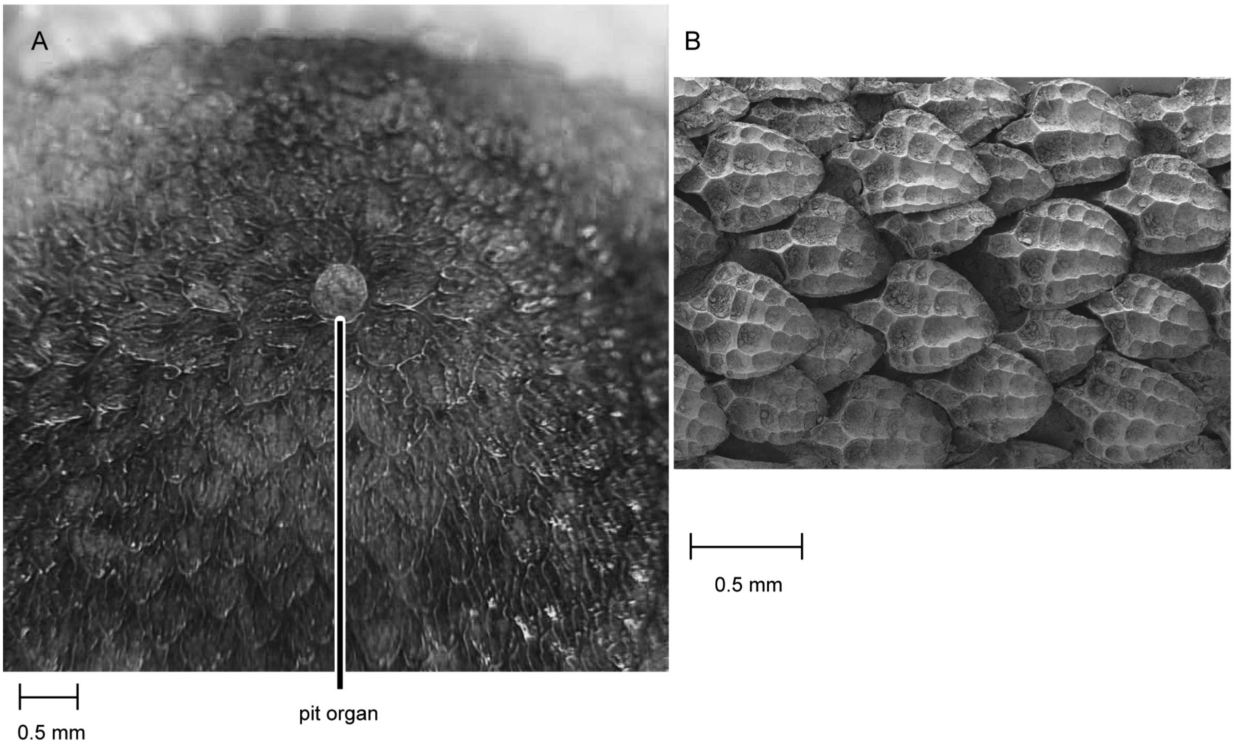

FIGURE 4. (A) Putative pit organ of *Mollisquama mississippiensis* **sp. nov.** in the photo center (0.5 mm diameter); anterior is the photo upper margin. (B) SEM micrograph of *Mollisquama mississippiensis* **sp. nov.** dermal denticles; anterior is to the left.

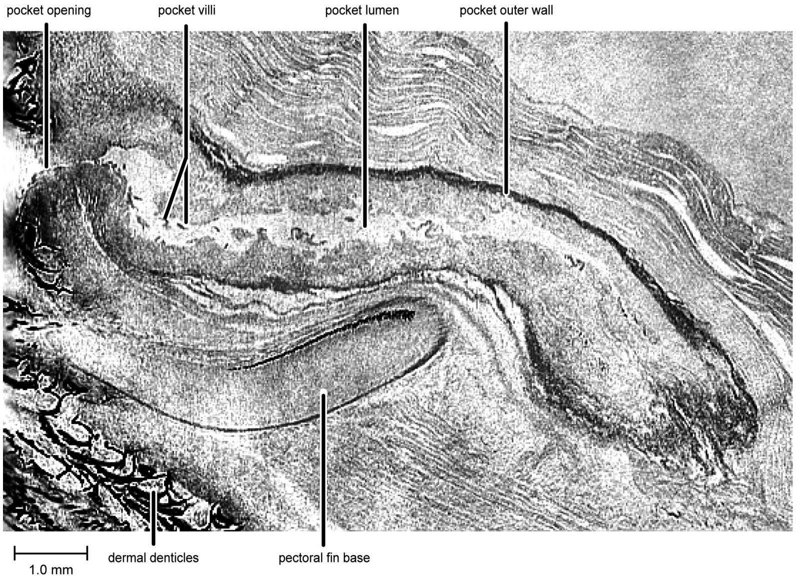

FIGURE 5. *Mollisquama mississippiensis* **sp. nov.** right pocket gland anatomy at maximum dimensions (a single synchrotron scan layer); total length approximately 7.0 mm x 1.5 mm width; anterior is to the right.

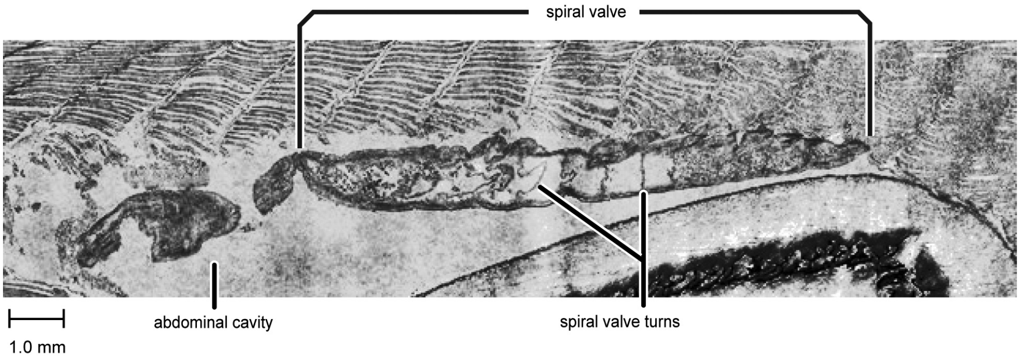

FIGURE 6. *Mollisquama mississippiensis* **sp. nov.** spiral valve detail (a single synchrotron scan layer); anterior is to the right.

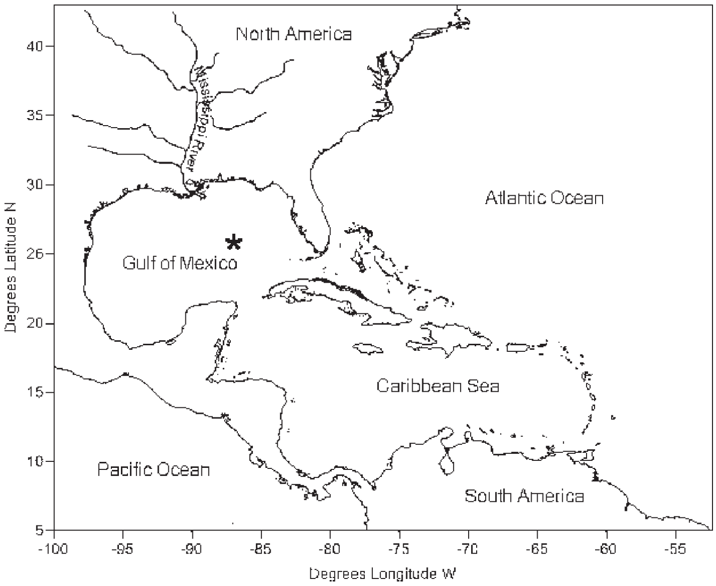

FIGURE 7. *Mollisquama mississippiensis* **sp. nov.** capture site (*).

Discussion

Differences that separate *M. mississippiensis* **sp. nov.** from *M. parini* that might be associated with ontogeny or sexual dimorphism could not be assessed or attributed to dalatiid ontogeny or sexual dimorphism. *Mollisquama mississippiensis* **sp. nov.** was found to have several cranial features that may prove to be apomorphic for the genus (Denton *et al*. 2018) and possibly for the new species once detailed comparisons with *M. parini* are made. *Mollisquama mississippiensis* **sp. nov.** is the only representative of the genus *Mollisquama* that has been subjected to molecular phylogenetic analysis (based on NADH2 gene sequences; Grace *et al*. 2015; Denton *et al*. 2018) and it is the only available specimen which to base the new species description; the holotype *M. parini* was not available for inspection (A. Baluskin, pers. comm.). The features that separate the two *Mollisquama* species are therefore based on comparison of *M. mississippiensis* **sp. nov.** with the published description of *M. parini* which is complete and accurate (A. Baluskin, pers. comm.). Even though there is uncertainty regarding *Mollisquama* spp. genetic variation, for some dalatiids with relatively broad biogeographical distributions there is evidence of both low (e.g., *Dalatias lichia*) and high (e.g., *Isistius* spp.) genetic divergence across the Isthmus of Panama (G. J. P. Naylor, unpublished); *Dalatias* + *Isistius* is the sister clade to *Mollisquama* + euprotomicrinine taxa (Denton *et al*, 2018). Additionally, within Squaliformes the two families that have examples of bioluminescence are relatively speciose (i.e., Etmopteridae has 46 species and Somniosidae has 18 species; https://sharksrays.org) with several examples of endemism (though not always geographically isolated from their congeners).

TABLE 1. Dalatiid vertebral counts (vertebral count classifications grouped by precaudal and caudal centra; Springer and Garrick 1964; Ebert *et al.* 2015).

Species	Reference	Monospondylous centra	Diplospondylus centra	Total centra
Mollisquama parini Pocket Shark	Dolganov 1984	42	41	83
Mollisquama mississippiensis ***sp. nov.*** American Pocket Shark	Grace *et al*. 2019	37	36	73
Squaliolus laticaudus Spined Pygmy Shark	Springer and Garrick 1964 Seigel 1978	44 – 47 27 – 32	13 26 – 32	60 55 – 62
Squaliolus aliae Smalleye pigmy shark	de Figueiredo and Carvalho 2018	29	30	59
Isistius brasiliensis Cookiecutter Shark	Springer and Garrick 1964 Ebert *et al.* 2015	60 – 66 62	20 – 25 18+	81 – 89 80
Isistius plutodus Largetooth Cookiecutter Shark	Springer and Garrick 1964 Stehmann & Kukuev 2014	65 43 – 45	27 48+ – 50	92 91 – 95
Euprotomicrus bispinatus Pygmy Shark	Hubbs *et al*. 1967 Springer and Garrick 1964	31 – 32 46 – 51	28 – 38 13 – 15	60 – 70 61 – 64
Dalatias licha Kitefin Shark	Springer and Garrick 1964	50 – 51	27 – 28	78 – 79
Heteroscymnoides marleyi Longnose Pygmy Shark	Springer and Garrick 1964 de Figueiredo and Carvalho 2018	52 33	18 33	70 66
Euprotomicroides zantedeschia Taillight Shark	Stehmann & Krefft 1988 Stehmann *et al*. 2016	46 45 – 46	32 – 40 35 – 40	78 – 86 80 – 86

For widely-distributed dalatiids that are well represented in collections, vertebral counts can vary by as many as 7 monospondylous and 6 diplospondylous vertebrae (e.g., *I. brasiliensis*; $n = 239$, de Figueiredo & de Carvalho 2018). By contrast *Mollisquama* spp. are relatively rarely encountered ($N = 2$) compared to most other dalatiids; however, the total vertebral count for *M. mississippiensis* **sp. nov.** is 10 fewer vertebrae than *M. parini* (Dolganov 1984) for a total count of 73. Pre-caudal monospondylous vertebrae are established early in embryonic development while the last caudal diplospondylous vertebrae form later in embryonic life (Springer & Garrick 1964). *Mollisquama mississippiensis* **sp. nov.** was a neonate past the embryonic stage so its vertebral formation was complete but the terminal caudal vertebrae may not have been fully mineralized because vertebral counts differed between the radiograph (Grace *et al*. 2015) and CT scans. The previously published diplospondylous counts from radiographs was 31 diplospondylous caudal centra (Grace *et al*. 2015) vs. the CT scan count of 36 (Fig. 3) that resolved terminal caudal vertebrae that may not have been completely mineralized. It should be noted that for *M. parini* the radiograph of vertebrae would have been made with equipment in use between 1979 and 1984 (Dolganov 1984), and the resolution of minute terminal vertebrae may not have been optimal compared to contemporary CT scanning; the *M. parini* vertebral count may be a minimum count. Additionally, accurate vertebral counts for other dalatiids also can be affected by radiograph resolution (e.g., Hubbs *et al.* 1967; *Isistius plutodus* diplospondylous vertebrae 48+, Stehmann & Kukuev 2014; *Isistius brasiliensis* precaudal vertebrae 18+, Ebert *et al.* 2015; Table 1).

The features of dentition that separate *M. mississippiensis* **sp. nov.** from *M. parini* must be considered with caution as they could be the consequence of undocumented ontogeny, sexual dimorphism, allometry, or locality (Springer 1964; Gilbert 1967; Kato *et al*. 1967; Taniuchi 1970; Straube *et al*. 2008). In addition, there were differences in features of the dentition depicted by photographic and synchrotron images. From the lower tooth photograph for *M. mississippiensis* **sp. nov. -** (Fig. 2), the shallow notches along the cusp margin and root striations (not present on *M. parini*) are not considered to be reliable distinguishing features since they were not seen on the synchrotron images (Denton *et al*. 2018). It should be noted the tooth photo was of removed right-lower erupted tooth #4 and the synchrotron image was for unerupted replacement left-lower tooth #4. The upper jaw tooth count is also not considered a distinguishing feature even though it differs between *Mollisquama* spp. (*M. mississippiensis* **sp. nov.** 10-1-10, and *M. parini* 11-1-11); it is not uncommon for dalatiids to have broader tooth count differences (e.g., Garrick & Springer 1964, Seigel 1978).

There is no evidence that pit organs are affected by ontogeny or sexual dimorphism in elasmobranchs, therefore the presence of the putative pit organ set on a neuromast in *M. mississippiensis* **sp. nov.** and the apparent lack of such an organ in *M. parini* further suggests they are two distinct species. Until the collection of *M. mississippiensis* **sp. nov.**, the occurrence of pit organs set on neuromasts as is documented for batoid rays (Peach & Marshall 2009; Klimley 2013) was unknown in sharks. The denticles surrounding the putative pit organ in *M. mississippiensis* **sp. nov.** are arranged radially around the putative "pit" (Fig. 4A) whereas they are typically oriented on a rostral-caudal axis in batoids (Peach 2003; Peach & Marshall 2009). A histological examination is required to assess the putative pit organ's properties (J. Marshall, pers. comm.).

The presence of photophores is considered to be a distinguishing feature of *M. mississippiensis* **sp. nov.** as they were not recorded for *M. parini* (Dolganov 1984). Photophores have been documented within other members of the Dalatiidae and within the only other family with well-documented photophore descriptions, the lanternsharks (Etmopteridae). Etmopterids serve as a useful comparison basis for photophores since so little is known about dalatiid bioluminescence, though phylogenetic analysis suggests the two groups may have acquired the trait independently (Hubbs *et al*. 1967; Reif 1985; Claes & Mallefet 2008; Straube *et al*. 2010). For etmopterids, photophore development first occurs during shark embryogenesis with fluorescent vesicle development prior to birth (Claes & Mallefet 2008). Additionally, photophore density, distribution pattern, degree of luminosity and kinetics can vary with ontogeny and sex, and photophore aggregations can have clade-specific patterns (Straube *et al*. 2010; Claes *et al*. 2014). The complete absence or presence of photophores (as compared between the two species of *Mollisquama* spp.) is not characteristic of etmopterid ontogeny or sexual dimorphism and has not been documented for dalatiids, however, the effects of preservation may contribute to not being able to discern photophores (J. Claes, pers. comm.; de Figueiredo Petean & de Carvalho 2018).

Ontogenetic allometry is documented for many elasmobranchs including squaloid sharks (e.g., Garrick 1960), therefore inferences of species separation based on morphological ratios may be misleading since the two known *Mollisquama* specimens are represented by an immature male neonate (142 mm TL, *M. mississippiensis* **sp. nov.**) and a mature female (400 mm TL, *M. parini*). Even though dalatiid newborns are fully-formed young that are miniatures of the adults, the distal proportions of *M. missssissippiensis* **sp. nov.** (e.g., head and caudal fin lengths) are greater than those of *M. parini* (Grace *et al*. 2015) which is a proportional difference often attributed to ontogenetic allometry for other squaloids (Garrick 1960). However, there are 18 morphometric proportional differences between the two species that exceed a comparative basis of +/- 5% (a percentage used in Grace *et al*. 2015 for developing a discussion of differences) with 14 of those differences exceeding +/- 20% (six of those percentage differences were not affected by distal proportions; Table 2).

Most of the internal features were not inspected by specimen dissection due to the rarity and fragile state of the specimen and the need to maintain it intact for additional imaging. Therefore, high resolution synchrotron scans (inspected by scrolling through scan layers) were used to examine the pocket gland (Fig. 5) and the two other internal organs that were documented in the holotype description, the spiral valve (Fig. 6) and the bilobed liver. The *M. mississippiensis* **sp. nov.** pocket gland inner cavity is lined with numerous villi that are visible in scan layer composite images (37 scan layers resolved 329 possible villi; approximately 0.2–0.4 mm total length), but villi could not be conclusively counted due to difficulties for discerning closely-set individual villi and the likelihood that some villi were laid flat against the pocket gland inner wall. The *M. mississippiensis* **sp. nov.** spiral valve has at least 17 turns (the holotype of *M. parini* has 23 spiral valve turns, Dolganov 1984), but due to abdominal compression and contortion from preservation the spiral valve turn count may be unreliable. From the synchrotron scans it is apparent that the liver shape was also affected by the abdominal compression and contortion but the liver appears to be bilobed; however, it could not be digitally isolated based on its tissue density.

The *M. mississippiensis* **sp. nov.** right-side pocket gland was further examined by histological sectioning. The pocket villi were found to be highly fluorescent and encapsulated by a pigmented layer surrounded by muscles (J. Claes pers. comm.). This suggests the pocket is analogous to the pocket of *E. zantedeschia* as a secretory gland that

TABLE 2. Comparison of morphometric values that exceeded +/- 5% between *M. mississippiensis* **sp. nov.** and *M. parini*. TOT = total length, HDL = head length, SNTT = snout tip to feature measurement, * measurement not affected by distal proportions; %TOT and %HDL from Table 1 in Grace *et al*. 2015.

Feature	*M. mississippiensis* **sp. nov**. %TOT (142.0 mm)	*M. mississippiensis* **sp. nov.** %HDL (33.9 mm)	*M. parini* %TOT (400.0 mm)	*M. parini* %HDL (73.2 mm)	*M. mississippiensis* **sp. nov.** % difference from *M. parini*
Dorsal fin 1 to dorsal fin 2	8.7		11.8		-26.2*
Dorsal fin 2 to caudal fin upper lobe	11.6		9.5		+20.5*
Pectoral fin origin to pelvic fin origin	27.5		37.3		-26.4*
Pelvic fin to caudal fin lower lobe	19.0		14.0		+35.5*
SNTT eye orbit	29.1		27.4		+6.1
SNTT gill slit 5	23.9		18.3		+30.5
SNTT pelvic fin	50.5		61.0		-17.2
Eye length	4.1		3.3		+25.0
Interorbital width	10.6		8.0		+32.0
Mouth width (lower corners)	6.3	26.6		32.9	-19.3
Gill slit #5 height	1.5	6.3	1.9	10.3	-21.0* TOT and -39.2 HDL
Pocket gland opening	3.0	12.5	3.0	16.4	-24.0 HDL
Pectoral fin anterior margin	9.9	41.4	11.5	63.0	-14* TOT and -34.3 HDL
Dorsal fin 1 base	5.4		6.0		-9.7*
Dorsal fin 2 base	6.3		7.5		-16.0*
Pelvic fin base	5.4		9.3		-41.5*
Caudal fin upper lobe	23.2		19.5		+19.1
Caudal fin lower lobe	14.0		11.5		+21.1

can be contracted to eject a luminous fluid (Munk & Jørgensen 1988). Additionally, a photophore aggregation (ventral row four, center aggregation between the pectoral fins, Fig. 1B) was visually examined (J. Claes pers. comm.) and showed structures similar to dalatiid photophores as described by Hubbs *et al*. (1967), Claes *et al*. (2014) and Straube *et al*. (2015) however, the photophores (approximately 100 microns diameter) were too damaged from freezing and preservation for histological sectioning. Furthermore, there are small dark spots distributed on many other areas of the body (Grace *et al*. 2015) that superficially resemble the photophores of the photophore aggregation. Therefore, based on the pocket gland histology and the visual assessment of a photophore aggregation it can be concluded that *M. mississippiensis* **sp. nov.** is a bioluminescent elasmobranch.

Conclusion

Mollisquama mississippiensis **sp. nov.** is distinguished from *M. parini* by five features that cannot be accounted for by ontogeny or sexual dimorphism. Additionally, there are 10 fewer vertebrae than *M. parini* and six morphometric proportional differences that vary from the holotype by +/- 20% that are not affected by ontogenetic allometry for distal features that is often characteristic of squaloid sharks; the vertebral count and morphometric differences are potential distinguishing features. *Mollisquama mississippiensis* **sp. nov.** and *M. parini* were collected from different habitats that are influenced by differing oceanographic conditions–*M. parini* from an area of the Pacific Ocean known for its isolation and high degree of endemism (Parin *et al*. 1997). The accession of *M. mississippiensis* **sp. nov.** has led to important dalatiid-characterization advances including a considerable range extension for the genus *Mollisquama*, the first report of a putative pit organ set on a neuromast from a squaliform shark, detailed imagery of the highly specialized pocket gland and confirmation of its bioluminescent properties, a new report of photophores for a dalatiid, and the broadest degree of dalatiid character transformations (eight) based on phylogenetic analysis and character optimization (Denton *et al.* 2018; two dental, two chondrocranial, three jaw, one muscular).

Etymology for *Mollisquama mississippiensis* sp. nov.

The Latin specific epithet is in recognition of the vast North American Mississippi River Basin (Fig. 7); a biologically and geographically rich region that nurtures Gulf of Mexico fauna and unites diverse cultures. The proposed common name is the American Pocket Shark in recognition of the extraordinary Americas of the Western Hemisphere.

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