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Huffmanela markgracei sp. n. (Nematoda: Trichosomoididae) from buccal cavity of Atlantic sharpnose shark, *Rhizoprionodon terraenovae* (Carcharhiniformes: Carcharhinidae), in the northwestern Gulf of Mexico off Texas

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Abstract: Eggs of *Huffmanela markgracei* sp. n. infected one of three Atlantic sharpnose sharks, *Rhizoprionodon terraenovae* (Richardson) (Carcharhiniformes: Carcharhinidae) captured by bottom long-line in the northwestern Gulf of Mexico off Padre Island, Texas. Eggs in the skin formed sinuous tracks (1–8 eggs wide; 1–4 eggs deep; 150 eggs/mm^2) occupying a swath of the skin 22 cm × 2 cm on the tongue, branchial arches and the dorsal surface of the buccal cavity. Eggs had transverse eggshell ridges (branching and non-branching), had shells that were clear, amber or brown, and measured 90–113 µm ($x = 102 \pm 4$; n = 190) long, 38–54 µm (43 ± 3; 190) wide, 3–5 µm (4 ± 0; 190) in eggshell thickness with protruding polar plugs 8–12 µm (10 ± 1; 190) wide. Apparently fully developed larvae in eggs were 255–335 µm (299 ± 26; 30) long, 8–10 µm (9 ± 1; 30) wide, and in-folded 5–6 (6 ± 0; 30) times. Some of these larvae were emerging from eggs in the skin. The new species differs from congeners by the combination of having a large, spindle-shaped egg, transverse eggshell ridges, an envelope that is smooth, tightly-apposed to the eggshell and surrounds the entire eggshell inclusive of the polar plugs, and a large larva. This is the first report of a species of *Huffmanela* Moravec, 1987 from a chondrichthyan in the Gulf of Mexico and from a shark not assigned to *Carcharhinus*.

Keywords: nematode, eggs, skin, taxonomy

Huffmanela Moravec, 1987 comprises 18 nominal species of histozoic, extra-intestinal nematodes whose adults deposit eggs in the skin, gill, somatic musculature, swimbladder, bone and mesentery (Ruiz et al. 2013). Six of those plus one unnamed species (MacLean et al. 2006) reportedly infect the skin only (Bullard et al. 2012, Ruiz et al. 2013) and most *Huffmanela* spp. (13 of 18) are described without obtaining adult specimens and based upon morphology of those eggs only. In October 2011, an Atlantic sharpnose shark, *Rhizoprionodon terraenovae* (Richardson) (Carcharhiniformes: Carcharhinidae), captured off Padre Island, Texas, was observed to have scribble-like markings in the buccal cavity. Similar markings have been observed casually on the body surfaces of other sharks from the Gulf of Mexico (CFR and SAB, observed casually by the present authors), but as of yet these have remained undiagnosed in the primary literature. Herein, we describe these markings in Atlantic sharpnose shark as an infection by a new species of *Huffmanela*. This is the first report of a species of *Huffmanela* from a cartilaginous fish (Chondrichthyes) in the Gulf of Mexico and from a shark not assigned to *Carcharhinus*.

MATERIALS AND METHODS

The infected Atlantic sharpnose shark (male, 937 mm total length, 3.6 kg) was captured by a bottom long-line set on 15 October 2011 off south Texas (26°59'53.70"N, 96°38'39.72"W, approximately 73 km east of Padre Island, Texas), northwestern Gulf of Mexico, aboard the *F/V Simple Man*. In the field, a skin biopsy from the shark's tongue was excised and stored in 10% neutral buffered formalin (n.b.f.), the infected area of the buccal cavity was photographed and the shark was frozen whole before being delivered to Auburn University (4 November 2011), where it was thawed in 10% n.b.f. (23 January 2012) and necropsied (29 November 2012).

In the laboratory, the general body surface, buccal cavity, branchial arches and underlying musculature, gill filaments of hemibranchs, interbranchial septa, body cavity, serosa, mesentery, alimentary tract, heart, liver, kidney, spleen, and somatic musculature were examined with a stereomicroscope for the presence of eggs, larval nematodes and adult nematodes. The head was separated from the body and the lower jaw was removed to facilitate examination of the buccal cavity surface. Infected areas of the skin were excised and photographed with the aid of a stereomicroscope.

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Eggs were wet-mounted on coverslipped glass slides and photographed using a compound light microscope equipped with differential interference contrast (DIC) optical components (Bullard et al. 2012, Ruiz et al. 2013). All nematode eggs and larvae were measured with an ocular micrometer with aid of a 100× oil immersion objective, 2× magnifier and DIC. Illustrations of eggs and larvae were facilitated with a drawing tube. Eggs for scanning electron microscopy (SEM) were processed by dehydration through a graded ethanol series, desiccation in hexamethyldisilazane for 3 hrs followed by evaporation for 1 hr, mounted on metal stubs using two-sided sticky tape and sputter-coated in gold. Morphometrics are reported in micrometres (µm) as a range followed by the mean ± standard deviation (SD) and sample size (n) in parentheses.

RESULTS AND DISCUSSION

Huffmanela markgracei sp. n. Figs. 1–21

Description of egg (190 clear, amber and brown eggs; SEM of several eggs): Egg field forming a broad swath 22 cm in maximum length and 2 cm in maximum width across portions of tongue, third sinistral gill arch, fifth dextral gill arch and dorsal surface of buccal cavity (Fig. 1), not extending to a gill filament or interbranchial septum, comprising clusters of thousands of eggs as well as extensively sinuous egg 'tracks' (Figs. 1, 2), approximately 150 eggs/mm^2, readily separating from buccal cavity surface as sheet-like, scale-less mass of putative epidermal cells and nematode eggs. Egg tracks up to 8 eggs in maximum breadth and 4 eggs in maximum depth, flanking or encircling base of placoid scales (Fig. 2).

Eggs spindle-shaped (Figs. 4–13, 15), approximately bilaterally symmetrical, with probable host cells adhered to surface of some eggs (Fig. 15). Eggshell clear, amber, or brown (Fig. 3), 3–5 (4 ± 0; 190) thick, having inner and outer layers in all examined eggs (Figs. 4, 5); outer layer, approximately 3 thick at poles of clear, amber, and brown eggs, decreasing to < 1 wide at egg equator, typically translucent; inner layer approximately 3 thick at equator of clear, amber and brown eggs, narrowing to approximately 1 at egg poles, typically dark-colored.

Envelope tightly-apposed (inner surface of envelope apposed to outer surface of eggshell such that no space is evident between envelop and eggshell), present in all examined eggs, surrounding entire egg inclusive of polar plugs in all examined eggs (Figs. 4–9). Thin filaments lacking. Eggshell ridges (Figs. 7, 13) present in all examined eggs, transverse, branching or non-branching (Fig. 17), 30–40 per egg hemisphere, pronounced such that envelop also appears ridged (Figs. 4–9, 15, 17), well-developed in clear, amber and fully-developed eggs with brown shells (Figs. 4–14).

Polar plugs typically protruding (Figs. 4–7, 10–13) in clear, amber or brown eggs, plugs 13–22 (19 ± 2; 190) long (length measured from apex of plug to nearest vitelline mass margin within egg lumen; see Remarks); non-protruding in 10 of 190 (5%) brown eggs (Figs. 8, 9, 15, 16). Clear-shelled eggs 97–109 (102 ± 3; 30) long, 40–44 (42 ± 1, 30) wide, few in number, lacking well-formed larva (Figs. 4, 10); vitelline mass 51–60 (57 ± 3; 30) long, 29–34 (32 ± 1; 30) wide, comprising nearly all egg content, lacking polar indentations; polar plugs 9–11 (10 ± 0; 30) wide. Amber-shelled eggs 90–113 (101 ± 5; 80) long, 39–54 (43 ± 3; 80) wide, enclosing developing larvae (Figs. 5, 11); vitelline mass diminished relative to clear eggs; luminal space accommodating larva 50–70 (59 ± 5; 80) long, 30–44 (33 ± 3; 80) wide; polar plugs 8–10 (9 ± 1; 80) wide. Brown-shelled eggs 99–109 (103 ± 3; 80) long, 39–49 (43 ± 2; 80) wide, numerous relative to clear-shelled eggs (Figs. 6, 12), having fully-developed larvae, 3 of 80 (4%) hatching in epidermis (Fig. 9; cf. Fig. 17 of Ruiz et al. 2013); vitelline mass greatly diminished relative to clear-shelled eggs or nearly lacking; luminal space enclosing larva 50–70 (61 ± 4; 80) long, 29–35 (32 ± 2; 80) wide; polar plugs 8–12 (10 ± 1; 80) wide. Fully-developed larva (Figs. 6, 8, 9) extruded from eggs in skin of tongue and branchial arches; body of larva 255–335 (299 ± 26; 30) long, 8–10 (9 ± 1; 30) wide, in-folded 5–6 times (6 ± 0; 30) within egg, transverse cuticular ridges indistinct with light microscopy; oesophagus approximately 1 wide.

Putatively non-viable eggs 54–91 (77 ± 9; 50) long, 33–50 (40 ± 3; 50) wide, lacking discernible larva (Figs. 18–21); eggshell clear or yellow, with transverse eggshell ridges, typically with dark inner layer and translucent outer layer (Figs. 20, 21) or with indistinct inner and outer layers (Figs. 18, 19); envelope tightly-apposed, surrounding entire egg inclusive of polar plugs; vitelline mass 40–60 (48 ± 4; 50) long, 27–40 (32 ± 2; 50) wide; polar plugs 6–11 (9 ± 1; 50) wide.

Male and female: Unknown.

Type host: *Rhizoprionodon terraenovae* (Richardson) (Carcharhiniformes: Carcharhinidae), Atlantic sharpnose shark.

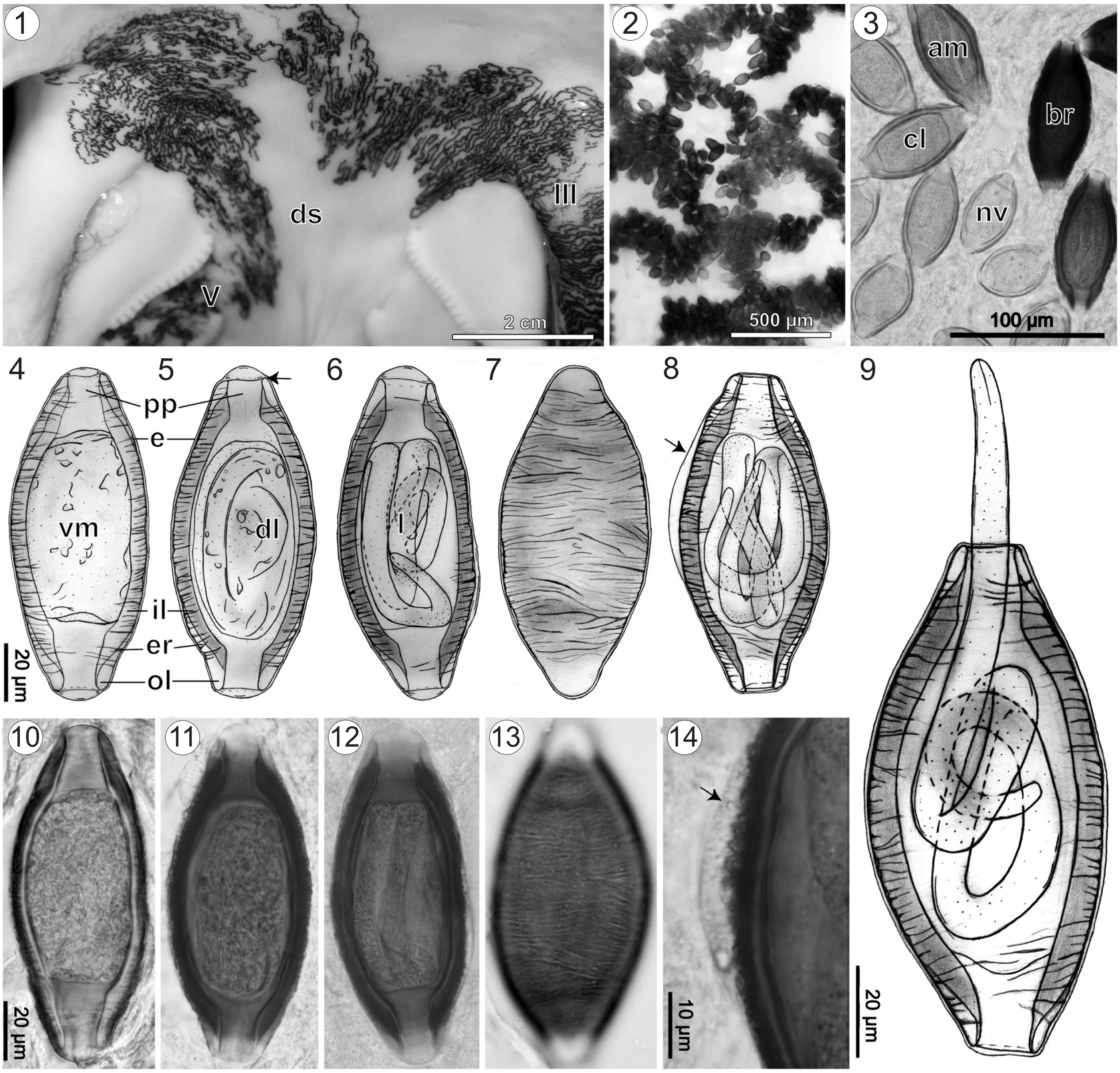
Type locality: Northwestern Gulf of Mexico (26°59'54"N, 96°38'40"W), approximately 73 km east of Padre Island, Texas.

Site of infection: Eggs in skin of tongue, branchial arches and posterodorsal buccal cavity.

Prevalence and intensity: Several thousand eggs of *H. markgracei* sp. n. infected 1 of 3 Atlantic sharpnose sharks examined.

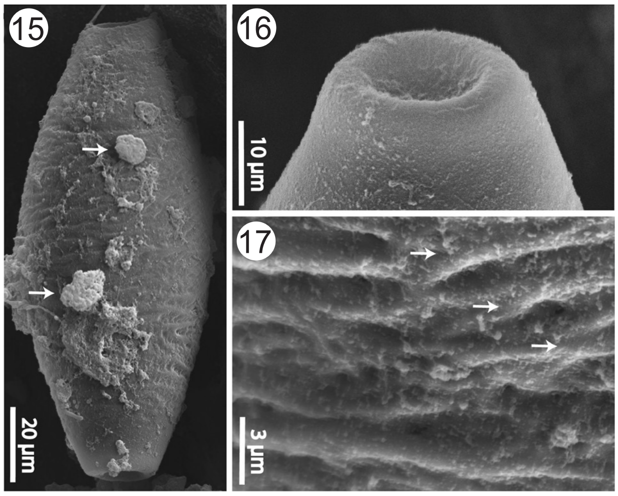
Deposition of type specimens: Syntypes, United States National Parasite Collection (USNPC No. 106967); syntypes Institute of Parasitology, Biology Centre of the Academy of Sciences of the Czech Republic, České Budějovice (N-1012).

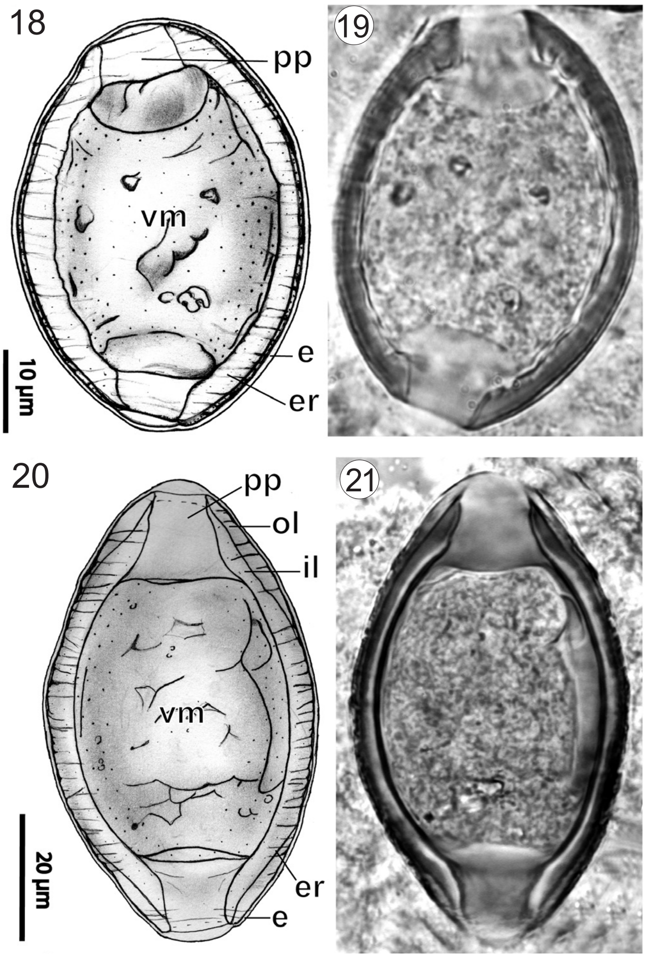
Etymology: The Latin specific epithet honours Mr. Mark Alan Grace (Fisheries Biologist, Southeast Fisheries Science Center, National Oceanic and Atmospheric Administration, Pascagoula, Mississippi, USA) for his contributions to fisheries science in the Gulf of Mexico and especially to our knowledge of elasmobranchs there.



Figs. 1–14. *Huffmanela markgracei* sp. n. (Nematoda, Trichosomoididae) from the skin of Atlantic sharpnose shark, *Rhizoprionodon terraenovae*. Scale values aside each bar. **Fig. 1.** Eggs in buccal cavity. **Fig. 2.** Eggs on tongue. **Fig. 3.** Higher magnification view of wet-mounted eggs from tongue. **Fig. 4.** Clear-shelled egg. **Fig. 5.** Amber-shelled egg with developing larva. **Fig. 6.** Brown-shelled egg with fully developed, highly in-folded larva. **Fig. 7.** Surface of brown-shelled egg showing transverse eggshell ridges. **Fig. 8.** Fully larvated brown-shelled egg under slight cover-slip pressure showing non-protruding polar plugs and envelope (arrow). **Fig. 9.** Hatching egg. Figs. 10–13. Light micrographs of the formalin-fixed, wet-mounted eggs illustrated above them. All same scale. **Fig. 10.** Clear-shelled egg. **Fig. 11.** Amber-shelled egg. **Fig. 12.** Brown-shelled egg. **Fig. 13.** Fully-developed, brown-shelled egg showing transverse eggshell ridges. **Fig. 14.** Higher magnification view of envelope (arrow) of egg in Fig. 8. *Abbreviations*: am – amber-shelled egg; br – brown-shelled egg; cl – clear-shelled egg; dl – developing larva; ds – dorsal surface of buccal cavity; e – tightly-apposed envelope; er – transverse eggshell ridges; il – dark inner eggshell layer; l – larva; nv – putatively non-viable egg; ol – clear outer eggshell layer; pp – protruding polar plug; vm – vitelline mass; III – third sinistral gill arch; V – fifth dextral gill arch.

Remarks. The new species differs from its congeners by the combination of having a long, spindle-shaped egg (90–113 µm; 102 ± 4; n = 190), transverse eggshell ridges, an envelope that is smooth (aspinous), tightly-apposed to the eggshell, and surrounds the entire eggshell inclusive of the polar plugs (all eggs examined), and a large fully-developed larva, 255–335 µm long (299 ± 26.4; 30). Eggs of the new species are longer than nearly all other species of *Huffmanela*, except *Huffmanela shikokuensis* Moravec, Koudela, Ogawa et Nagasawa, 1998 (78–90 µm) and *Huffmanela banningi* Moravec, 1987 (99–108 µm), whose eggs infect the somatic muscle of filefishes (Mona-





Figs. 15–21. *Huffmanela markgracei* sp. n. (Nematoda, Trichosomoididae) from the skin of Atlantic sharpnose shark, *Rhizoprionodon terraenovae*. Figs. 15–17. Scanning electron microscopy of eggs. Scale values aside each bar. **Fig. 15.** Fully-larvated egg (confirmed with light microscopy before processing for SEM) with probable host cells (arrows) adhered to egg envelope. **Fig. 16.** Non-protruding polar plug of fully-larvated egg, possibly representing artifact. **Fig. 17.** Higher magnification view of transverse eggshell ridges, including some that are branched (arrows). **Fig. 18.** Putatively non-viable egg lacking distinct eggshell layering. **Fig. 19.** Light micrograph of egg in Fig. 18. **Fig. 20.** Putatively non-viable egg showing distinct eggshell layering. **Fig. 21.** Light micrograph of egg in Fig. 20. *Abbreviations*: e – envelope; er – transverse eggshell ridges; il – inner eggshell layer; ol – outer eggshell layer; pp – polar plug; vm – vitelline mass.

canthidae) and flatfishes (Cynoglossidae), respectively (see Table 1 of Ruiz et al. 2013).

The presence of eggshell ridges differentiates the new species from *H. shikokuensis* and *H. banningi*, which lack eggshell ridges. However, such ridges are not unique to the new species: *Huffmanela canadensis* Moravec, Conboy et Speare, 2005 has eggshell ridges that are transverse and slightly oblique (see Fig. 1O–P of Moravec et al. 2005), and *Huffmanela balista* Justine, 2007 has longitudinal eggshell ridges (see Fig. 3B,D of Justine 2007). The number of eggshell ridges might also be diagnostic: the new species has 30–40 per hemisphere, while *H. canadensis* seemingly has many fewer, approximately 10–13 per hemisphere (cf. Fig. 1K–R of Moravec et al. 2005). In addition, an unnamed species of *Huffmanela* has ovoid, not spindle-shaped, eggs that are 50–55 µm long and that have transverse eggshell ridges (see Fig. 2 of Conboy and Speare 2002). This species infects the skin of rock sea basses (*Sebastes* spp.) in the northwestern Pacific Ocean off British Columbia (Conboy and Speare 2002).

The eggshell in other congeners is smooth in *H. carcharhini* (MacCallum, 1925) Moravec, 1987, *H. huffmani* Moravec, 1987, *H. schouteni* Moravec et Campbell, 1991, *H. mexicana* Moravec et Fajer-Avila, 2000, *H. paronai* Moravec et Garibaldi, 2000, *H. branchialis*, *H. filamentosa* and *H. ossicola* Justine, 2004, *H. lata* Justine, 2005, *H. longa* Justine, 2007, spinous in *H. oleumimica* Ruiz et Bullard, 2013 and *H. moraveci* Carballo et Navone, 2007, with protuberances in *Huffmanela japonica* Moravec, Koudela, Ogawa et Nagasawa, 1998, or unspecified in *H. plectropomi* Justine, 2011.

The presence of an envelope differentiates the new species from *H. filamentosa*, *H. canadensis*, *H. longa*, *H. plectropomi*, *H. carcharhini* and *H. lata*, which all lack an envelope. In addition to envelop presence or absence, the envelope's shape, surface features and relationship with the eggshell are diagnostic, too. It can be spinous in *H. banningi* – van Banning 1980, Moravec 1987, and *H. huffmani* – Žďárská et al. 2001, adorned with protuberances (*H. schouteni* – Moravec and Campbell 1991), pliable and of irregular thickness in advanced eggs (*H. japonica* – see Fig. 1C of Moravec et al. 1998), lacking from the region of the protruding polar plug (*H. shikokuensis* – Moravec et al. 1998, and *H. mexicana* – see Fig. 1 of Moravec and Fajer-Avila 2000), variably present or absent in advanced eggs (*H. paronai* – see Fig. 1 of Moravec and Garibaldi 2000), spindle-shaped (*H. branchialis* – see Fig. 1A–E of Justine 2004), pliable with numerous filaments (*H. ossicola* – see Fig. 2 of Justine 2004), variably present, inconspicuous, thin and unornamented (*H. balista* – see Fig. 3 of Justine 2007), lightly ornamented and slightly separated from eggs (*H. moraveci* – see Figs. 11, 19 of Carballo and Navone 2007), and pliable, sac-like and loosely-apposed to the eggshell surface (*H. oleumimica* – see Figs. 8–13 of Ruiz et al. 2013).

The egg envelope of the new species is smooth and tightly-apposed to the eggshell, i.e. the envelope is not sac-like or pliable and surrounds the entire eggshell inclusive of the polar plugs. In addition, the body length of the fully-developed larva of the new species (255–335 µm [299 ± 26; 30]) exceeds that reported for most species of *Huffmanela*, but falls within the range of several species: *H. balista* (245–295 µm), *H. schouteni* (210 µm), *H. ossicola* (250 µm), *H. carcharhini* (188–273 µm), and *H. lata* (220–250 µm).

Huffmanela oleumimica is the only other nominal species of *Huffmanela* reported thus far from the Gulf of Mexico (Ruiz et al. 2013) and no previous study has reported an infected cartilaginous fish (Chondrichthyes) there. Moreover, no described species of *Huffmanela* has been reported previously from a shark not assigned to *Carcharhinus*. In comparing only species of *Huffmanela* that infect chondrichthyans, we observed no striking morphological similarity among them; however, the new species is most readily differentiated from *H. caracharhini* and *H. lata* by having eggshell ridges (Ruiz et al. 2013).

Caution is called for when measuring and comparing polar plug dimensions in species of *Huffmanela*. We considered the polar plug as the structure that blocks the tunnel-like hole, or bore, through which the larva emerges from the egg. We have not observed a live egg of a species of *Huffmanela*, but we surmise that the shape of the polar plug reflects its function, perhaps analogous to a champagne bottle cork that is laterally-expanded proximally within the container's lumen. Regarding 'polar plug width', we measured it as the diameter of the tunnel-like hole it fills; the laterally-expanded proximal portion of the plug that is within the egg lumen is wider and presumably of variable width depending on larval development. Presumably, the width of the tunnel reflects body width of the fully-developed larva (Fig. 9).

Regarding 'polar plug length', we measured it as the distance from the outer (apical) surface of the polar plug to its proximal base, which apposes the egg's contents, i.e. vitelline mass or mature larva depending on egg age. It would seem intuitive that the polar plug shortens as the larva within the egg develops. Hence, we did not use this length measurement as justification for differentiating the new species. A less intraspecifically variable length measurement may be the length of the tunnel through which the larva emerges, perhaps more accurately termed 'tunnel length'. Although not necessarily 'polar plug length' sensu stricto, this measurement is likely to be decoupled from egg developmental stage (= egg age).

Documenting the continuum of larval development from the clear egg that encloses vitelline material and no discernable larva to the fully-larvated egg that is dark-shelled and encloses an obvious fully-formed larva is important regarding the taxonomy of *Huffmanela* spp. Indeed, this continuum could be the general pattern of egg development in *Huffmanela*. However, diagnostic features of eggs of *Huffmanela* spp. should derive mainly from larvated eggs because non-viable eggs can appear distinctive and co-occur with larvated eggs on the same host individual. For example, herein, we observed several anomalous eggs in the skin of the infected sharpnose shark: these eggs were markedly smaller, more spheroid (not spindle-shaped) and unembryonated (Figs. 3, 18, 19). We inferred that they were non-viable conspecifics because they had transverse eggshell ridges, were surrounded by larvated eggs of the new species (Fig. 3) and lacked larvae themselves; however, direct morphometric comparisons alone would suggest they were not eggs of *H. markgracei*. To our knowledge, the only other description of a species of *Huffmanela* that has treated non-viable eggs is that of *H. plectropomi* (see Justine 2011). As such, we advocate basing species descriptions primarily on viable and larvated eggs, supplemented with morphometric data on and illustrations of developing eggs. Yet, the matter is not so logistically or practically simple because the eggshell of some mature eggs of some species of *Huffmanela* is black, making confirmation of a larva within that egg impossible without crushing, clearing, or sectioning the egg. Perhaps a solution to this conundrum is to measure those eggs and follow-up with a destructive method that at least confirms the egg holds a mature larva.

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