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Research Article

A Third Luminous Shark Family: Confirmation of Luminescence Ability for *Zameus squamulosus* (Squaliformes; Somniosidae)

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ABSTRACT

Since recently, shark's bioluminescence has been recorded from two Squaliformes families, the Etmopteridae and Dalatiidae. Pictures of luminescence, light organ morphologies and physiology of the luminous control have been described for species of the Etmopteridae and Dalatiidae families. In 2015, a third luminous family, Somniosidae, was assumed to present a bioluminescent species, *Zameus squamulosus*. Up to now, confirmation of the luminous abilities of *Z. squamulosus* is lacking. Here, the luminescence of *Z. squamulosus* was *in vivo* recorded for the first time confirming the bioluminescence status of the third luminescent shark family. Additionally, photophore histology revealed the conservation of the light organ morphology across the luminous Squaliformes. Light transmittance analysis through the placoid scale added information on the luminescence efficiency and highlighted a new type of bioluminescent-like squamation. All these data reinforced the likelihood that the common ancestor of Dalatiidae, Etmopteridae and Somniosidae may already have been luminescent for counterillumination purpose.

INTRODUCTION

Bioluminescence, the ability to emit visible light by a living organism, has been recorded for two deep-sea Squaliformes families to date, the Etmopteridae and the Dalatiidae (1). Even if homologies can be noticed regarding light organs (*i.e*. photophores) morphology and physiological control of light emission, particularities are present for each family (1). Etmopteridae present a diversified luminous pattern with zones suggested to play different functions such as the ventral zone emitting light for counterillumination purposes (2), flank marks, claspers and dorsal pattern for conspecific recognition, reproduction and schooling (3,4), and spine-associated luminous zones serving as an aposematic signal (4,5). Embedded within the shark epidermis, photophores are morphologically well conserved among *the Etmopterus* genus and are composed of photogenic cells (*i.e,*. photocytes) encased in a cup-shaped pigmented structure coated with a reflective layer of guanine crystals (6,7). At the photophore top, facing the outside, an iris-like structure (ILS) made of interspersed pigmented cells surmounted by lens cells is present (6,7). The ILS serves as a photophore shutter via pigment motions (8,9). Etmopteridae luminescence is produced intrinsically even if the luminous system remains to be discovered (10). Comparatively, in Dalatiidae, luminescence is mainly produced ventrally hence the function seems to be only restricted to counterillumination (11); light emission occurs in photophores presenting a unique photocyte and a less dense or absent ILS (12–14). Up to now, all studied luminous sharks present a singular hormonal control of the light emission (8,9).

In 2015, based on a review of photophore presence in Squaliformes, *Zameus squamulosus*, the velvet dogfish, was assumed to be a luminous species (15). Straube et al., revealed small dark circular skin spots attributed to photophores; this observation leads to the statement that Somniosidae represents the third luminous Squaliformes family. Surprisingly, *Z. squamulosus* does not present needle-, hook-, cross-shaped or pavement-like squamation considered by Reif, 1985, as the typical bioluminescent-like squamation for luminescent sharks (16–18), but rather harbor overlapping leaf-shaped tricuspid placoid scales (15). To allow efficient light propagation and transmission, these scales were assumed to be translucent (15). Nevertheless, up to now, clear evidence of light emission for this species is lacking and photophore histology and scales transmittance have yet to be established.

A little is known about the biology and-life history characteristics of this shark. *Z. squamulosus* is a scarce but wide-ranging deep-water shark recorded in the Atlantic, Pacific and Indian oceans from near the surface to 2000 m depth (19–21). Adult male sizes range from 47 to 51 cm, while adult females are bigger reaching 59 to 69 cm (19-21). The biggest velvet dogfish recorded is of 84 cm (22). The shark diet is mainly composed of small fishes, squids and shrimps (23). Viviparous, this species has a litter of 3 to 10 pups and no reproductive seasonality has been detected so far (19–21,23). Vertical segregation has been suggested to occur in Hawaiian waters since only female were caught at similar depth (23) and circadian migration has been suggested for this species (19).

Here, the luminescence of *Z. squamulosus* was *in vivo* recorded for the first time confirming its bioluminescent status. Additionally,

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photophore histology revealed the conservation of the light organ morphology across the luminous Squaliformes. Analysis of the light transmittance through the placoid scale added information on the luminescence efficiency and underlined a new type of bioluminescent-like squamation. All these data not only confirmed that Somniosidae contains a luminous species but also reinforced the likelihood that the common ancestor of Dalatiidae, Etmopteridae and Somniosidae may already have been luminescent for counterillumination purpose, as it is suggested to be the most basal bioluminescence function in sharks.

MATERIALS AND METHODS

Specimen sampling. Two adult female specimens of *Z. squamulosus* [53 and 83 cm total length (TL) for 910 and 2820 g, respectively] were caught during a field session (campaign Chatham Rise fish survey, R. V. Tangaroa, NIWA) in January 2020 by trawl off the coast of New Zealand. By-catch specimens maintained in a tank with fresh cold sea water in a dark cold room were photographed in dim daylight conditions (24 mm lens, 1000 ISO, f2.5, speed 1/10 sec) and in the dark (24 mm lens, 65535 ISO, f1.4, speed 30 sec) via a Sony α7SII camera before having a full incision of the spinal cord at the level of the first vertebrae, according to the European regulation for animal research handling and experimental fish care. Skin patches of 5 cm^2 were dissected from the ventral area (between the pectoral fins), the lateral side area (the flank of the specimen) and dorsal area (in front of the first dorsal fin), fixed in phosphate buffer saline (PBS) —paraformaldehyde 4% overnight, then stored in PBS until use.

Photophore density and histology. Skin patches were observed and photographed under a transmitted light microscope (Leitz Diaplan, Germany) coupled with a ToupCam camera (UCMOS Series C-mount USB2.0 CMOS camera, ToupTek, Zhejiang, China). Photophores' diameter and their density (counted per mm^2) were measured after careful removal of placoid scales.

For histology, skin tissues were bathed in PBS with increasing sucrose concentrations (10% for 1h, 20% for 1h and 30% overnight), placed in small plastic chambers, embedded in optimal cutting temperature compound (O.C.T. compound, Tissue-Tek, The Netherlands) and rapidly frozen at −80°C. A cryostat microtome (CM3050S, Leica, Solms, Germany) was used to obtain 10 µm sections across skin tissues. Sections were laid on coated slides (Superfrost, Thermo Scientific) and left to dry. Sections were observed under a transmitted light and epifluorescent microscope (Leitz Diaplan) equipped with a ToupCam camera (ToupTek).

Placoid scale light transmission. To analyze the light transmission across *Z. squamulosus* placoid scales, ventral skin was immersed in a 2.5% hypochlorite solution during two to three hours until dermal scales detach from the remaining integument tissue. Isolated scales were then rinsed in artificial sea water (ASW) before being mounted on glass slides in a frame-seal incubation chamber (SLF060, BioRad, United Kingdom) containing ASW. Light transmission across the scale was evaluated with a spatial accuracy of 10 µm by illuminating uniformly the scale from underside in a Köhler configuration with a blue LED source (between 452 and 504 nm) mimicking the shark light emission. An objective allows an optical magnification about 20 times and forms an image on a plane where the light flux is collected by an optical fiber of 0.1 mm^2 aperture, mounted on two x-y motorized stages. The light is eventually guided to a grating spectrometer (Ocean Optics) where the spectral intensity is recorded with a wavelength resolution of 0.25 nm. The characterization of the physical property sought through the placoid scale analysis concerns the spectral energy transmittance $T(\lambda)$, or transmission coefficient, of a light intensity $I_0(\lambda)$ of wavelength arriving perpendicularly on the scale surface, allowing only an intensity $I(\lambda)$ to pass across, according to the simple relation:

$$T(\lambda) = \frac{I(\lambda)}{I0(\lambda)}$$

From the spatial and spectral data, the transmission coefficients of different parts of the scale can be deduced. To extract the local and spectral transmittance $Tscale(x,y,\lambda)$ specific to the scale, it is first necessary to eliminate from the total transmitted intensity $Isignal(x,y,\lambda)$, the intensity fluctuations due to the spatial and spectral inhomogeneities of the light source $Isource(x,y,\lambda)$ as well as the residual background illumination $Idark(x,y,\lambda)$ arriving on the spectrometer optical fiber. The contribution to the total absorption due to the slide presence and the sample holder is evaluated by measuring in the same way the total transmittance $Isupport(x,y,\lambda)$ in absence of scale. The transmission of the scale is eventually given by the ratio of the total transmission to the transmittance of the support:

$$Tscale = \frac{Tsignal}{Tsupport} = \frac{(Isignal - Idark)/(\mathrm{Isource} - Idark)}{(Isupport - Idark)/(Isource - Idark)}$$

By integrating on small spectral bands $\Delta\lambda$, the reconstruction of transmission images by frequency band has been established. Then, for each of the defined zones on the scale, the spectral transmittances were deduced.

In parallel, scanning electron microscopy was performed on isolated placoid scales to describe the different structures. Scales were immersed

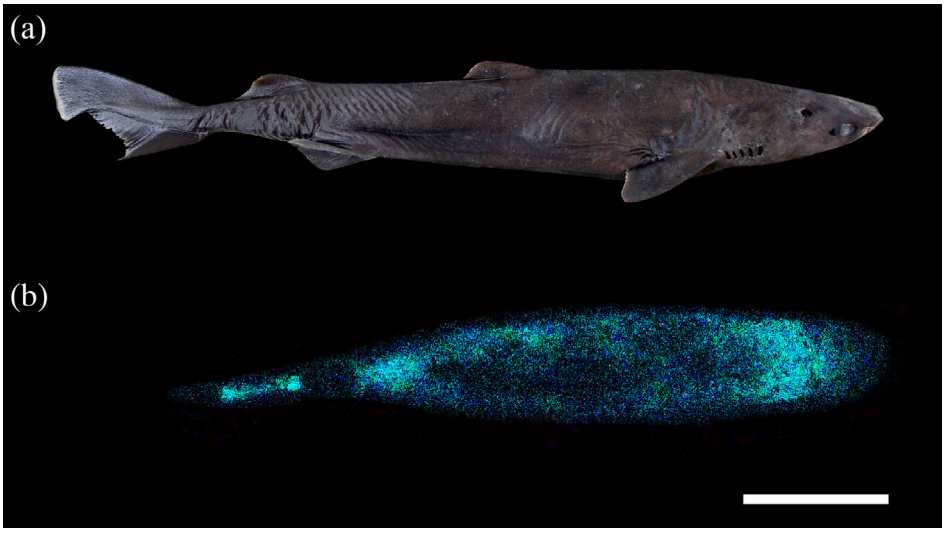

Figure 1. *Zameus squamulosus* pictures. (a) Lateral daylight and (b) ventral luminescence pictures. Scale bar represents 10 cm.

in graded ethanol, mounted on aluminum stubs, before being coated with gold in a sputter coater and observed with a JEOL JSM-6100 scanning electron microscope (JEOL Ltd., Tokyo, Japan).

RESULTS

Through the Chatham Rise fish survey onboard of the R. V. Tangaroa, the *Z. squamulosus* bioluminescence first observations were obtained. This deep-sea shark species, maintained in a fully dark environment, emitted a dim blue-green light from the ventral side of the body observable with dark adapted naked eye (Fig. 1).

Conversely to the Etmopteridae, specific patterns (*e.g.* flank marking, dorsal lines, fin-associated or sexual patterns; 3,4) were not present. The velvet dogfish luminous pattern was rather similar to the Dalatiidae ventral glow (13,14). Skin patches of *Z. squamulosus* presented a specific squamation with overlapping tricuspid leaf-shaped placoid scales. Beneath the ventral placoid scale felting, aligned clusters of small round-shaped black dots or rings (mean diameter 48.76 ± 6.29; $n = 75$) were spread (Fig. 2a-a″). A photophore density gradient is observed from the dorsal side (0.27 ± 0.40 photophore mm^{-2}; $n = 12$) to the ventral side of the shark (21.01 ± 3.82 photophore mm^{-2}; $n = 12$) with an intermediate value for the lateral area (8.00 ± 4.19 photophore mm^{-2}; $n = 12$). Scan electron microscopy images reveal the placoid scale to be around 700 µm long and 300 µm wide. The scale is anchored in the skin integument by a large base with an overhanging subepidermal leaf-shape structure (Fig. 2b), the upper scale surface harbors concave honeycomb zones in between each of the three crests (Fig. 2b′), while the underside view presents a smooth surface of the overhanging part and a four edges hollow base (Fig. 2b″). Ventral photogenic skin section analyses revealed the histology of the photophore structure: a unique photocyte embedded in a pigmented sheath within the epidermal layer (Fig. 2c), similar to the one observed in already studied luminous Dalatiidae species (15-17). Some photophores harbored a single layer of iris-like structure cells between the unique photocyte and the epidermis outside (Fig. 2c′), while no specific lens cells were observed. Functionality of photocyte was

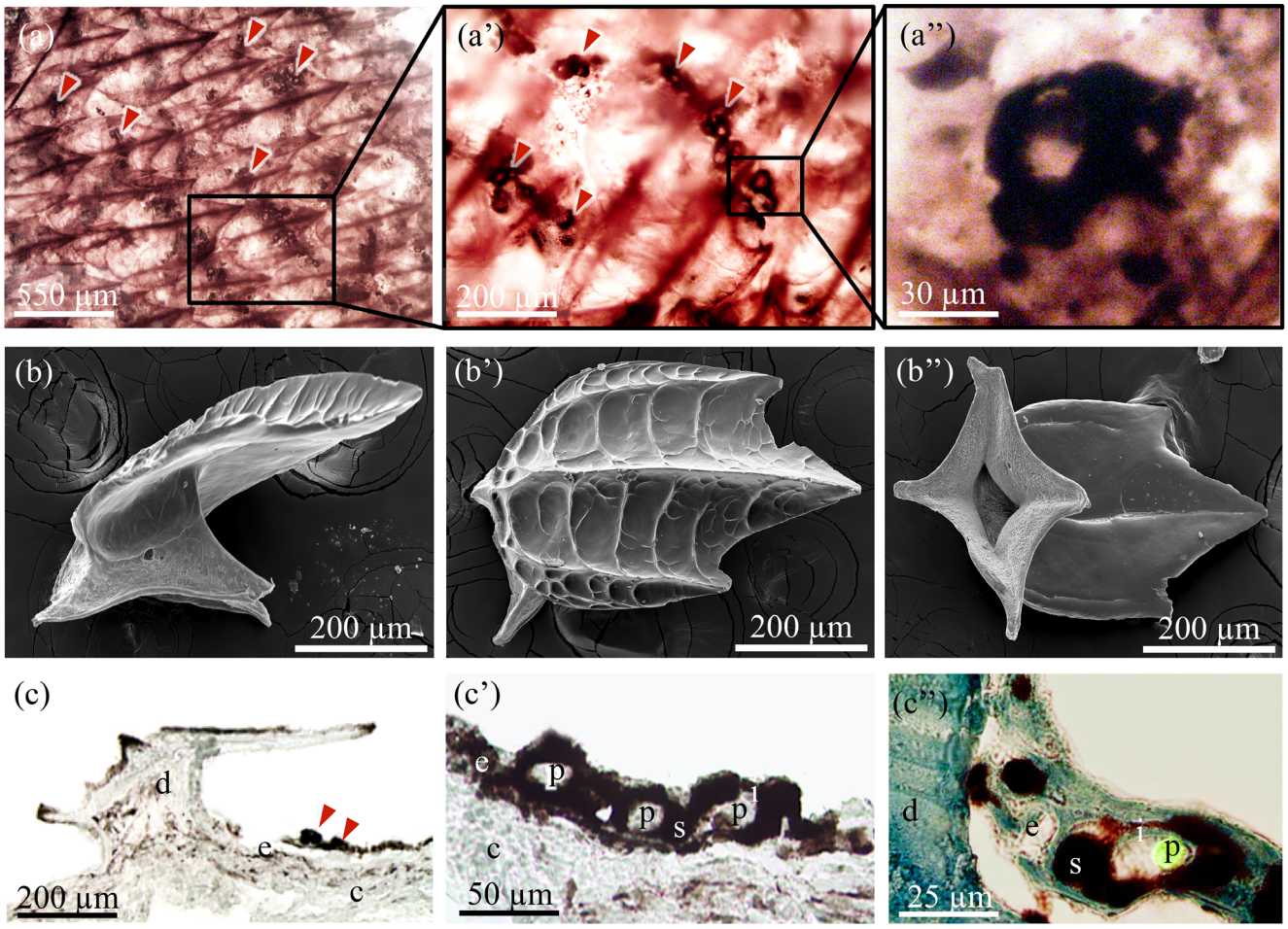

Figure 2. *Zameus squamulosus* photogenic and placoid scale structures from macroscopic to SEM description. (a) Specific squamation with overlapping tricuspid leaf-shaped placoid scales. (a′) Closer view of aligned small round-shaped photophores clusters (red arrowhead). (a″) Close-up of a photophore through honeycomb upper surface of the scale. (b) SEM lateral view of the overhanging leaf-shaped scale. (b′) SEM upper view of the scale showing the 3 crests and the honeycomb structures. (b″) SEM view from below of the four edges hollowed base and smooth underside of the leaf-shaped scale. (c) Transversal cryosection across the photogenic ventral skin presenting overhanging leaf-shaped scale and below photophores (red arrowhead). (c′) Close-up of ventral photophore cluster. (c″) Epifluorescent view of a photophore with a greenish autofluorescent photocyte. c: Connective tissue; d: placoid scale; e: epidermis; i: iris-like structure cells; p: photocyte; s: pigmented sheath.

assumed since this cell presented an observable greenish autofluorescence (Fig. 2c″) as depicted for the Etmopteridae photocyte in previous studies (24,25).

Analyses of the light transmission of the blue-green light mimicking the shark light emission across the new type of bioluminescent-related placoid scales revealed different transmission zones (Fig. 3a). For each determined zone (i.e. honeycomb and opaque crests), transmission coefficients were measured during underneath light exposure from wavelength of 452 to 504 nm (Fig. 3b); close examination of the crest and honeycomb structures revealed an increase of light transmission across the honeycomb surface while the crest did not present any modification and, and on the whole scale no obvious changes are observed (Fig. 3b). Combining the results from the range of wavelength analyzed, scales show an overall light transmission of only 25%. Differential analysis of the scale structure shows that this relatively low average transmittance is mainly due to the 10% transmission coefficient of the crest structure of the scale. On the contrary, the honeycomb interstitial areas, which are larger than the underneath skin photophores, present a much higher transmission coefficient, ranging from 40% toward blue and up to 50% approaching green wavelengths (Fig. 3a–c).

DISCUSSION

Bioluminescence of *Z. squamulosus* belonging to the third luminous shark family, the Somniosidae, is here described for the first time. Straube et al., by describing visual observation of black dot beneath the placoid scales, have assumed the bioluminescent status of this species (15).

Here, through bioluminescent live picture this status is confirmed. The velvet dogfish, *Z. squamulosus,* emit a blue-green light via photogenic organs comparable to Dalatiidae photophores, *that is*, a unique photocyte enclosed in a pigmented sheath and surmounted by few iris-like structure cells (12–14). Assumption is made on the intrinsic production of luminescence for this species, as for the Dalatiidae luminous representatives. As recently demonstrated for the velvet belly lanternshark, *Etmopterus spinax* (10), *Z. squamulosus* photophore histology does not highlight any typical tubular or glandular structure with aperture to the outside able to support a population of symbiotic bioluminescent bacteria (26).

Conversely to the known bioluminescent-like squamation, *that is,* pavement, needle/bristle-, cross-, hook-shaped placoid scales (16–18), *Z. squamulosus* presents a new type of bioluminescent-related squamation. Interestingly, the upper surface of the leaf-

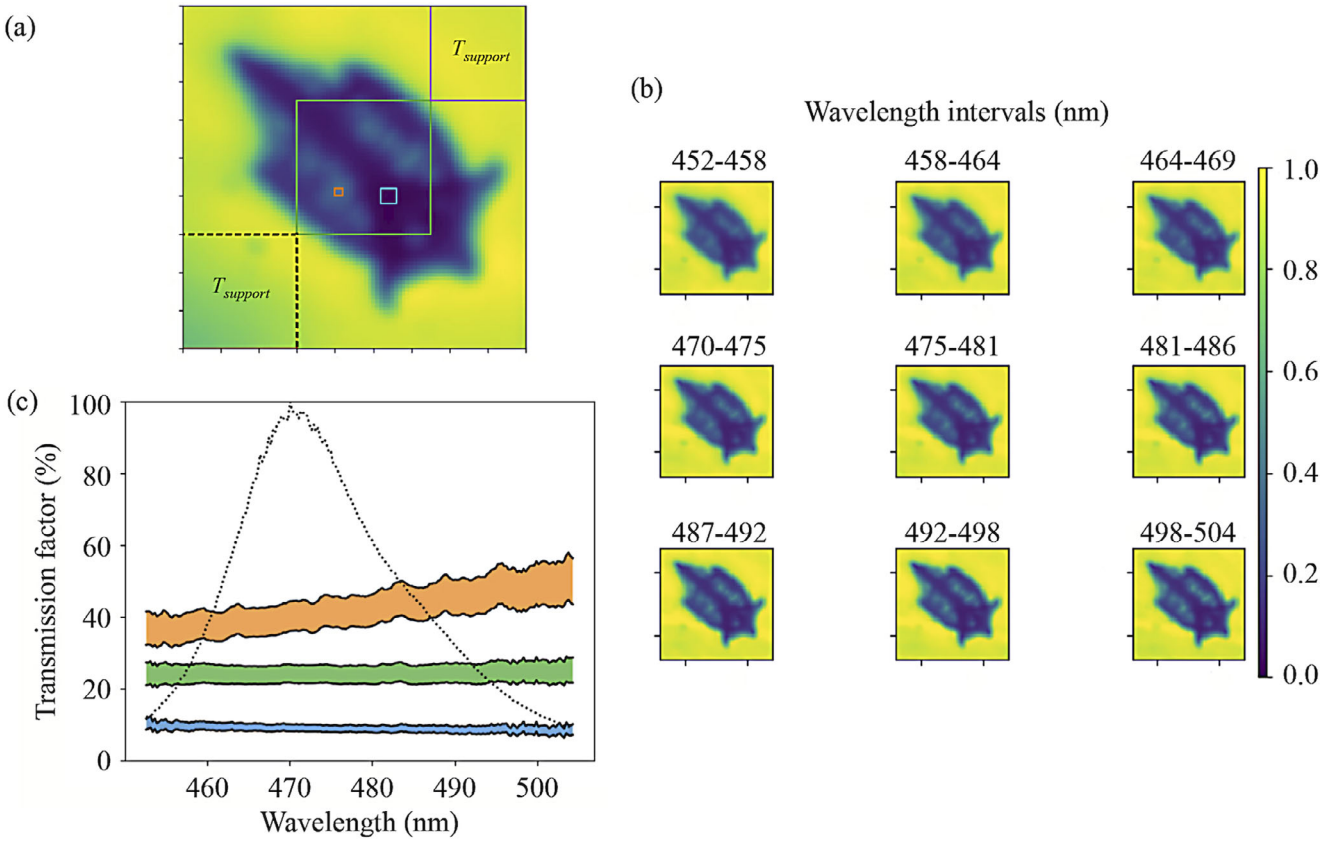

Figure 3. *Zameus squamulosus* placoid scale transmittance analyses. (a) Definition of the analyzed zones. The two squares outside the placoid scale define the reference zone of the transmittance of the support + solution (*Tsupport*). The small orange point is the pixel from which the transmittance of the honeycomb areas of the scale will be deduced after processing. The small blue square represents the crest area from which the transmittance has been deduced and the large central square, the average transmittance of the whole scale. (b) Spatial distribution of transmittance by spectral band within blue-green wavelength. The lateral scale indicates the color code corresponding to the value of the coefficient $T(\lambda \pm \Delta\lambda/2)$. (c) Transmission coefficients of honeycomb areas (orange), the crest opaque structure (blue) and the whole scale (green). Bands represent the 1—σ confidence interval for each area. The dashed curve represents the light source spectrum.

shaped scale displays specific honeycomb structures, the size of which (100 × 60 μm) being larger than the underneath photophores (50 μm), allowing the best transmission of the luminescence. In another tissue form a luminous shark, *E. spinax,* bioluminescence transmittance across the dorsal spine was evaluated to 10 % (5), while in a luminous Gasteropoda, *Hinea brasiliana*, through a specific shell architecture, the transmittance was measured to 63% (27). Comparatively in a nonluminous freshwater teleost, *Ctenopharyngodon idella*, a transmittance value of 20–30% was estimated for the dermal scale (28). Our value is in the high range of transmittance suggesting a significant role in light transmission. One hypothesis about the scale's structure function might be that the large tricuspid leaf-shape scale acts as a diffuser of light. The lack of any lens cells in the photophore and the small size of the photophore might have led to the coevolution of a specific squamation: scale, covering numerous photophores, with highly transmitting honeycomb zones and low transmitting ridges creating a uniform halo of light. This kind of overlapping placoid scales is already depicted for the rostral area of a Dalatiidae luminous shark, *Dalatias licha,* which present highly translucide leaf-shaped placoid scales without crest and honeycomb structures (14). The velvet dogfish, *Z. squamulosus,* emit a blue-green light mainly ventrally, as indicated by the photophores dorso-ventral density gradient, which might act as a counterillumination-type camouflage to avoid being spotted by underneath swimming predators (2,29–31). To confirm this assumption, further ethological and behavioral studies need to be implemented.

Regarding the phylogenetic position of *Z. squamulosus* and the remaining luminous shark families (Etmopteridae and Dalatiidae) within the Squaliformes phylogeny (15), two hypothesis arose concerning the bioluminescence origin in sharks: (i) bioluminescence abilities evolved multiple times in the Squaliformes evolutive history, or (ii) bioluminescence ability was present in a common ancestor, maintained in certain clades (Etmopteridae, Dalatiidae and Somniosidae) and lost in the remaining families. Our results brought not only for the first time bioluminescence proof for a Somniosidae species, but also evidence of a morphological conservation of the photophore structures between *Z. squamulosus* and Dalatiidae. Moreover, considering the common hormonal control mechanism in Etmopteridae and Dalatiidae (8,9,14,25), the second hypothesis being most likely. Further studies need to be conducted to address the physiological light emission control of the velvet dogfish *Z. squamulosus* to document whether a hormonal control of the bioluminescence, similar to that found in the two other luminous shark families (8,14), is found within this species, reinforcing the common evolution between these three families. Although recent studies discard either a symbiotic bacterial origin or a coelenterazine-associated luminous system for *E. spinax* (10,32), so far nature of light reaction remains unknown in Etmopteridae, Dalatiidae and Somniosidae representatives. This study provides the first evidence that the Somniosidae species, *Z. squamulosus*, glows in the dark. There is still work to undertake to understand the physiological control, the biochemical mechanism and the functions of bioluminescence in this shark. All these data will allow to decipher the evolutionary ways that led to the appearance of bioluminescence in Squaliformes.

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