

Bioluminescent-like squamation in the galeomorph shark *Apristurus ampliceps* (Chondrichthyes: Elasmobranchii)

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Abstract

Galeomorph sharks constitute the most taxonomically and ecologically diverse superorder of living selachians. Despite comprising several typically deep-water taxa, no bioluminescent species have been reported in this group so far. Interestingly, the study of shark squamation has been revealed in recent years to be a good proxy for inferring some ecological aspects of poorly known species. In particular, the high morphological specificity of the dermal denticles and the squamation patterns of all currently-known bioluminescent sharks could constitute a potential tool for predicting bioluminescence in both fossil and living taxa. Following this idea, we provide the first evidence supporting the possible existence of bioluminescence among galeomorph sharks by means of the quantitative study of *Apristurus ampliceps* squamation pattern. Classical morphometric analysis and multivariate statistical procedures have allowed us to determine that *A. ampliceps* squamation, composed mainly of bristle-shaped dermal denticles, is highly convergent with that of the bioluminescent shark *Etmopterus spinax*. The ecology of *A. ampliceps*, being a species that exclusively inhabits aphotic waters, is in agreement with such a morphofunctional interpretation, but finding photophores is imperative to confirm this prediction.

Contents

Introduction	187
Material and methods	188
Results	189
Discussion	191
Acknowledgements	194
References	194
Online supplementary information	196

Introduction

Bioluminescence is widespread in deep-water marine organisms, being present from bacteria to vertebrates, fulfilling diverse crucial functions (Haddock *et al.*, 2009; Widder, 2010). Among living sharks, this adaptation has been documented in three different families (i.e. Dalatiidae, Etmopteriidae and Somniosidae), all of them belonging to the Superorder Squalomorphii (Straube *et al.*, 2015 and references therein). In contrast, no evidence has been reported supporting its occurrence in the Superorder Galeomorphii, despite being the most diverse clade of sharks and comprising a number of groups with typically mesopelagic species (Martin and Treberg, 2002; Ebert *et al.*, 2013). *In vivo* studies are extremely difficult to perform in deep-water habitats and the presence of bioluminescence is usually inferred from indirect observations through the identification of photophores in captured specimens (e.g. Reif 1985a, b; Straube *et al.*, 2015). Unfortunately, these structures easily disintegrate and rarely persist in museum specimens. As a consequence, the discovery of new bioluminescent groups may have been hindered. This is supported by the existence of bioluminescence in the family Somniosidae that has not been noticed until very recently with the fortuitous discovery of photophores in *Zameus squamulosus* (Straube *et al.*, 2015), although this species was formally described in the 19th century (Günther, 1877).

Interestingly, squamation seems to be an alternative valuable source of functional and ecological information in sharks (e.g. Reif, 1982, 1985a, b; Ferrón *et al.*, 2014; Fletcher *et al.*, 2014; Dillon *et al.*, 2017; Ferrón and Botella, 2017). Placoid scales show a wide range of morphological variation being involved in

at least four different functions, including protection against abrasion, defense against ectoparasites and the settlement of epibionts, reduction of the skin friction drag and accommodation of photophores in bioluminescent species (see Reif, 1982, 1985a, b). Reif (1985a, b) and more recently Ferrón and Botella (2017) have studied the squamation patterns of a number of selachians demonstrating that the dermal denticles of bioluminescent sharks (i.e. dalatiids and etmopterids) show highly distinctive morphologies. Reif (1985a, b) described four different dermal denticle morphotypes exclusive to bioluminescent sharks, including (1) dermal denticles with concave facets forming a dense pattern (e.g. in *Isistius brasiliensis*, *Dalatias licha*, *Euprotomicrus bispinatus* and *Etmopterus schultzi*); (2) dermal denticles with long and bristle-shaped crowns (e.g. in *E. spinax*); (3) dermal denticles with long slender hook-shaped crowns (e.g. in *E. bullisi*, *E. hillianus*, *E. unicolor* and *E. lucifer*) and (4) comparatively widely spaced short thorn-like dermal denticles (e.g. in *Centroscyllium ritteri*, *C. fabricii* and *Etmopterus virens*) (compare those with the typical dermal denticle morphologies of non-bioluminescent sharks in the comprehensive work of Reif, 1985b). All these different morphologies respond to common selective pressures, offering alternative solutions to enable the accommodation of photophores and the passage of the light emitted by them. Later, Ferrón and Botella (2017) developed a useful quantitative approach that establishes the relationship between lifestyle and squamation in sharks in order to make ecological inferences in taxa poorly known from an ecological perspective. These authors characterized different morphotypes and functional types of placoid scales by means of morphometric and multivariate analyses and described the squamation pattern of several ecological groups of sharks (including those of bioluminescent species) considering both the distribution and the coverage areas occupied by each dermal denticle functional type. Based on this, we propose that the study of the squamation in deep-water taxa could become a useful alternative tool for exploring the presence of new possible bioluminescent groups and directing the search of photophores on specific taxa.

Apristurus spp. are suitable candidates for exploring the possible existence of bioluminescence in galeomorph sharks given that the vast majority of them are deep-water taxa with poorly known ecology. Here we carry out a detailed study of the squamation pattern of the Roughskin Catshark (*Apristurus ampliceps*), a species living on the continental slopes of southern

New Zealand and southern Australia that exclusively inhabits aphotic waters at depths ranging from 840 to 1500 meters. The inclusion of this species within the comparative framework developed by Ferrón and Botella (2017) has allowed the description of a squamation pattern highly convergent with that of some bioluminescent taxa, suggesting the possible evolution of bioluminescence among galeomorph sharks.

Material and methods

Three specimens of *Apristurus ampliceps* from the collections of the Australian Museum (Sydney, Australia) were examined (I.24355.002/1, I.26001-002 and I.24355-007). All of them were juvenile females ranging from 35 to 40 centimetres in total body length. Their squamation patterns were described qualitatively and quantitatively following the methodology developed by Ferrón and Botella (2017). Thus, the body surface of each specimen was virtually divided into several regions (dorso-lateral, ventral, and fins), the areas of which were represented separately on Cartesian coordinate systems. After that, a visual inspection under binocular microscope was performed in each specimen, noting and describing all the distinct dermal denticle morphologies and establishing the topological limits between them (transitional boundaries correspond to comparatively narrow regions between areas occupied by two different dermal denticle morphologies, which therefore are usually easy to delimit visually). In parallel, skin samples were taken from different topological positions using dermatological punches with a diameter of 2 and 3 mm and cleaned mechanically (using soft toothbrushes and distilled water at high pressure) and chemically (with sodium hypochlorite, NaOCl 5-6.5%) (following Reif, 1985b). Four dermal denticles of each specimen representing each of the distinct observed morphologies were then photographed in crown view using a Hitachi S4800 scanning electron microscope at the Central Service for Experimental Research of the University of Valencia, Spain. A classical morphometric analysis was then performed measuring a total of ten variables on the crown of each dermal denticle, some of which were later combined in order to generate adimensional variables (corresponding to the same set of variables established in Ferrón and Botella, 2017; Table 1). The dermal denticles were introduced as ungrouped specimens into Canonical Variate Analysis 1 (CVA-1) of Ferrón and Botella (2017) and assigned to

Table 1. Description of the variables measured on the crown surface of *Apristurus ampliceps* dermal denticles and the size-free variables included in the Canonical Variate Analysis-1 (CVA-1) performed by Ferrón and Botella (2017).

Measured variables	Variables in the analysis
MLC (Maximum Length of Crown)	MLC/MWC
MWC (Maximum Width of Crown)	RLA/MLC
RLA (Ridge Length Average)	RLA2/ACS
LLR (Length of the Longest Ridge)	(MLC*MWC)/ACS
LSR (Length of the Shortest Ridge)	LLR/MLC
ACS (Area of the Crown Surface)	(LLR-LSR)/MLC
CP (Crown Perimeter)	CP/MLC
Circularity [$4*\pi*(ACS/CP^2)$]	Circularity
Roundness [$4*ACS/(\pi*Major\ axis^2)$]	Roundness
Solidity (ACS/Convex area)	Solidity

one of the shark dermal denticle morphotypes and corresponding functional types considered in that work (i.e. dermal denticles that enable the accommodation of photophores, defensive dermal denticles against ectoparasites and epibionts, drag reduction dermal denticles, dermal denticles that protect against abrasion and dermal denticles with generalized functions; see Table S1). The ten morphometric measurements described above were considered as discriminant variables. This allowed the area covered by each morphotype and functional type to be calculated for all the studied specimens. Dermal denticles from circum-oral region or fin leading edges were also photographed and classified into functional types but their coverage percentages were not calculated as they usually cover negligible areas (Reif, 1985b; Ferrón and Botella, 2017). Finally, all three specimens of *A. ampliceps* were introduced into Canonical Variate Analysis 2 (CVA-2) also carried out by Ferrón and Botella (2017), considering as discriminant variables the percentage of coverage of each dermal denticle morphotype, and assigned to one of the six ecological groups of sharks established in that work (i.e. strong-swimming pelagic species, schooling species of low to moderate speed, demersal species on rocky substrates and in caves, demersal species on sandy and muddy substrates, mesopelagic luminescent species and slow species of the open water). The original CVA-1 was based on 56 dermal denticles, 21 of which belonged to bioluminescent sharks; whereas the original CVA-2 considered 56 different shark specimens, 8 of which

were bioluminescent taxa. Both CVAs have a high predictive power according to the high percentages of correctly classified cases in the cross-validation tests (Ferrón and Botella, 2017: tables 4 and 6). A detailed description of further methodological details can be found in Ferrón and Botella (2017). The measurements were taken with ImageJ software 1.46r and CVAs were performed using PASW Statistics 18 software. One specimen of the bioluminescent species *Etmopterus spinax* (I.30731-001, female, 28.5 centimetres) was also sampled, photographed and figured for comparative purposes (focussing on the degree of similarity regarding dermal denticle morphologies and the presence, distribution and body coverage of each dermal denticle functional type).

Results

The squamation of the all three specimens of *Apristurus ampliceps* shows up to four clearly different dermal denticle morphologies that occupy specific body areas (Figure 1A). The dermal denticles on the snout (morphology 1, M1) exhibit thickened rounded or leaf-shaped crowns ($\approx 250\ \mu\text{m}$ in width and $300\ \mu\text{m}$ in length), with no ridges or a weak central ridge (Figure 1A and Figure 2A) which becomes more pronounced posteriorly (Figure 2B and C). The dermal denticles are densely packed showing overlapping crowns (Figure 2B). The dermal denticles covering most of the remaining body surface (morphology 2, M2) have bristle-shaped crowns ($\approx 50\ \mu\text{m}$ in width and $300\ \mu\text{m}$ in length) curved in their most distal part (Figure 1A and Figure 2D-F). The morphology and arrangement of the dermal denticles situated on the dorsal and ventral body surface do not differ considerably, displaying in both cases very low densities without overlapping crowns (compare Figure 2D and E). The dermal denticles on the leading edge of the pectoral, pelvic, dorsal and anal fins (morphology 3, M3) have similar morphological features, all showing large rhomboidal crowns ($\approx 200\ \mu\text{m}$ in width and $300\ \mu\text{m}$ in length) with poorly developed ridges (Figure 1A and Figure 2G). These dermal denticles are densely packed, with overlapping crowns arranged parallel to the fin edge. Dermal denticles with leaf-shaped crowns, better-developed ridges, lateral wings and a less dense arrangement, are found towards the trailing edge (denticles situated in the left part of Figure 2G). Lastly, the dermal denticles on the leading edge of the caudal fin (morphology 4, M4) show large and robust crowns ($\approx 300\ \mu\text{m}$ in width and

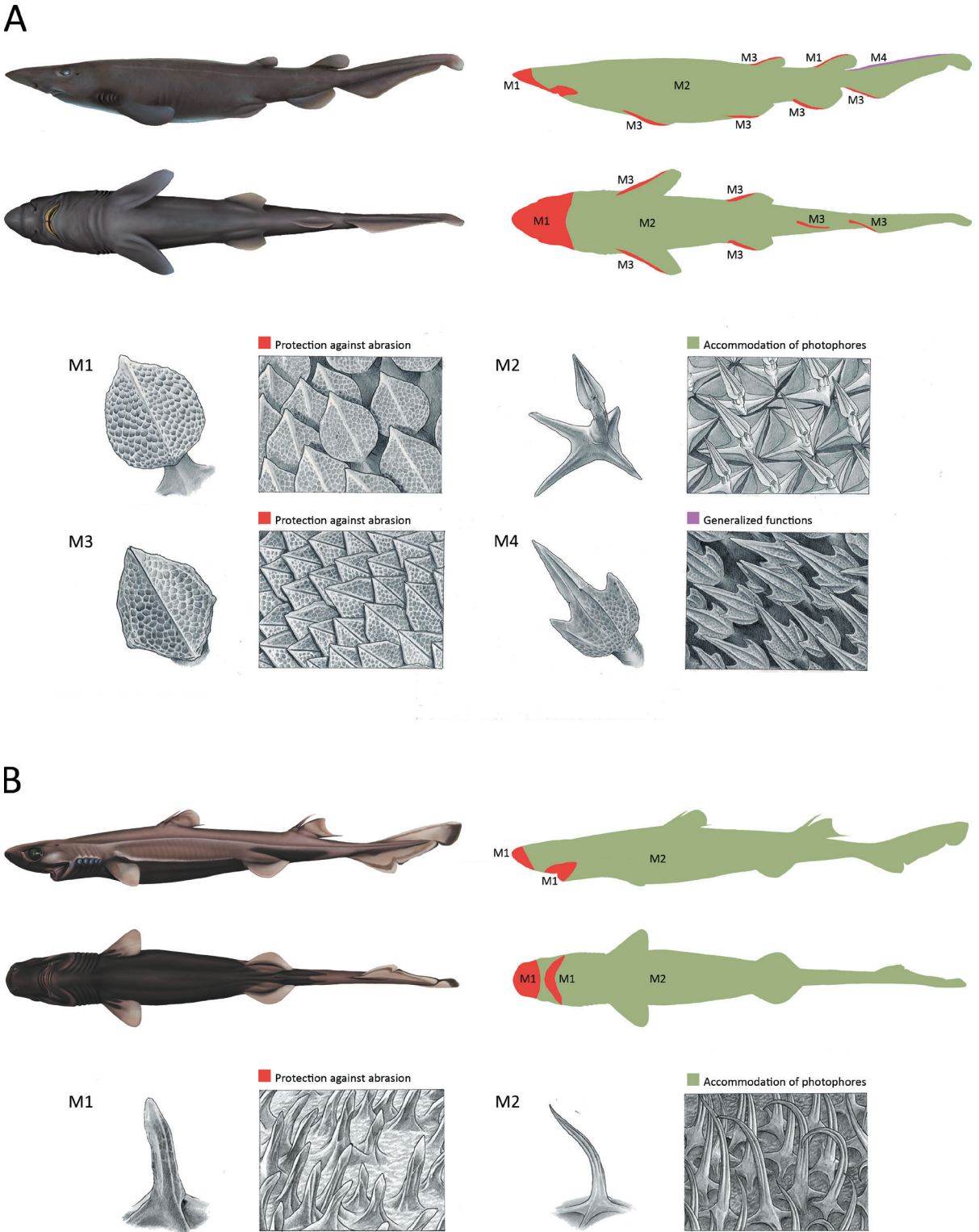


Figure 1. Squamation patterns of (A) *Apristurus ampliceps* and (B) *Etmopterus spinax* showing the body distribution and coverage of each dermal denticle morphology and functional type. *E. spinax* diagram based on information extracted from Ferrón and Botella (2017). Shark and dermal denticle drawings courtesy of Hugo Salais (HS Scientific Illustration).

400 μm in length) with well-developed lateral wings and two central ridges converging at the apex (Figure 1A and Figure 2H-I). These dermal denticles show a comparatively dense arrangement with some degree of crown overlap. Honeycomb-like ultrasculpture on the dorsal side of the crown is common in all dermal denticle morphologies. Gill septa are devoid of dermal denticles.

Morphometric measurements taken on M1-4 dermal denticles are shown in Table S2. After their inclusion in CVA-1, they were assigned to three different morphotypes and functional types corresponding to those described by Ferrón and Botella (2017); M1 and M3 dermal denticles were assigned to morphotype 6 (dermal denticles that protect against abrasion), M2 dermal denticles were assigned to morphotype 2 (dermal denticles that enable the accommodation of photophores), and M4 dermal denticles were assigned to morphotype 8 (dermal denticles with generalized functions) (Figure 3A and Table S2). Posterior probabilities (probability of belonging to the group) are high, very close to 1 in all cases. Mahalanobis distance to the centroid and conditional probabilities (probability of obtaining a discriminant punctuation as obtained or more extreme within the group) of *A. ampliceps* dermal denticles are similar to those of the morphotypes and functional types to which they were assigned, except for some M4 dermal denticles (conditional probabilities ranged from 0.52 to 0.85 in M1; from 0.14 to 0.66 in M2; from 0.38 to 0.88 in M3; and was lower than 0.1 in all M4) (compare Table S2 with Ferrón and Botella, 2017: S6 Table C). Together, these results indicate that the assignments of *A. ampliceps* dermal denticles into morphotypes and functional types were reliable. The estimated body coverage percentages of each morphotype and functional type were very similar for the three studied specimens of *A. ampliceps* (Table S3). After their inclusion in CVA-1, they were assigned to the ecological group of mesopelagic luminescent species with high reliability, as indicated by the posterior probability values as well as by the Mahalanobis distances to the centroid (Figure 3B and Table S3).

Discussion

The potential to use squamation as an indicator of the ecology and lifestyle of sharks has already been noticed by previous authors (e.g. Reif, 1985a, b; Ferrón *et al.*, 2014; Fletcher *et al.*, 2014; Dillon *et al.*, 2017; Ferrón

and Botella, 2017). In particular, Reif (1985a, b) suggested that the high specificity of the dermal denticle morphology of etmopterids and dalatiids could become a powerful tool for predicting bioluminescence in both living and extinct taxa. In fact, Reif (1982) anticipated the presence of bioluminescence in *Dalatius licha* based on the morphological similarity of its dermal denticles with those of other bioluminescent sharks, which was confirmed in later work with the detection of photophores (Reif, 1985a). However, the lack of quantitative studies in this regard has prevented more reliable ecological inferences or predictions based on statistical procedures from being made. The recent development of methodologies based on morphometric techniques and multivariate analysis has established a key tool to address this issue (Ferrón *et al.*, 2014; Dillon *et al.*, 2017; Ferrón and Botella, 2017; see also Raschi and Musick 1986; Raschi and Tabit, 1992; Gilligan and Otway, 2011; Motta *et al.*, 2012), offering an alternative approach for assessing the ecology of poorly known deep-water species and, more particularly, enabling the detection of potential previously unacknowledged cases of bioluminescence. Even so, indirect inferences made by the study of the squamation pattern should be always cautiously considered as only the detection of photophores is a valid criterion to confirm the presence of bioluminescence in new taxa.

Here, the qualitative and quantitative analysis of the squamation pattern of *Apristurus ampliceps* juveniles supports a high convergence with the bioluminescent shark *Etmopterus spinax*. The similarity is especially noticeable in the distribution and the body coverage percentages of the different dermal denticle functional types (Figure 1 and Table S3) as well as in the density, length/width crown ratio and crown curvature of dermal denticles located in the dorso-lateral and ventral regions (i.e. M2 dermal denticles) (compare Figure 2D-F and Figure 2K-L). In fact, morphometric analyses and CVA results support a highly reliable assignment of *A. ampliceps* to bioluminescent sharks (Figure 3B and Table S3) and the inclusion of M2 dermal denticles into a morphotype of “bioluminescent” dermal denticles, which is exclusive to *E. spinax* (Figure 3A and Table S2). Other aspects of the squamation of *A. ampliceps* clearly differ from those of *E. spinax* such as the presence of dermal denticles with generalized functions in the dorsal edge of the tail and the existence of abrasion resistant dermal denticles in an important area of the head and the leading edges of the remaining fins, which may be suggestive of a more benthic lifestyle.

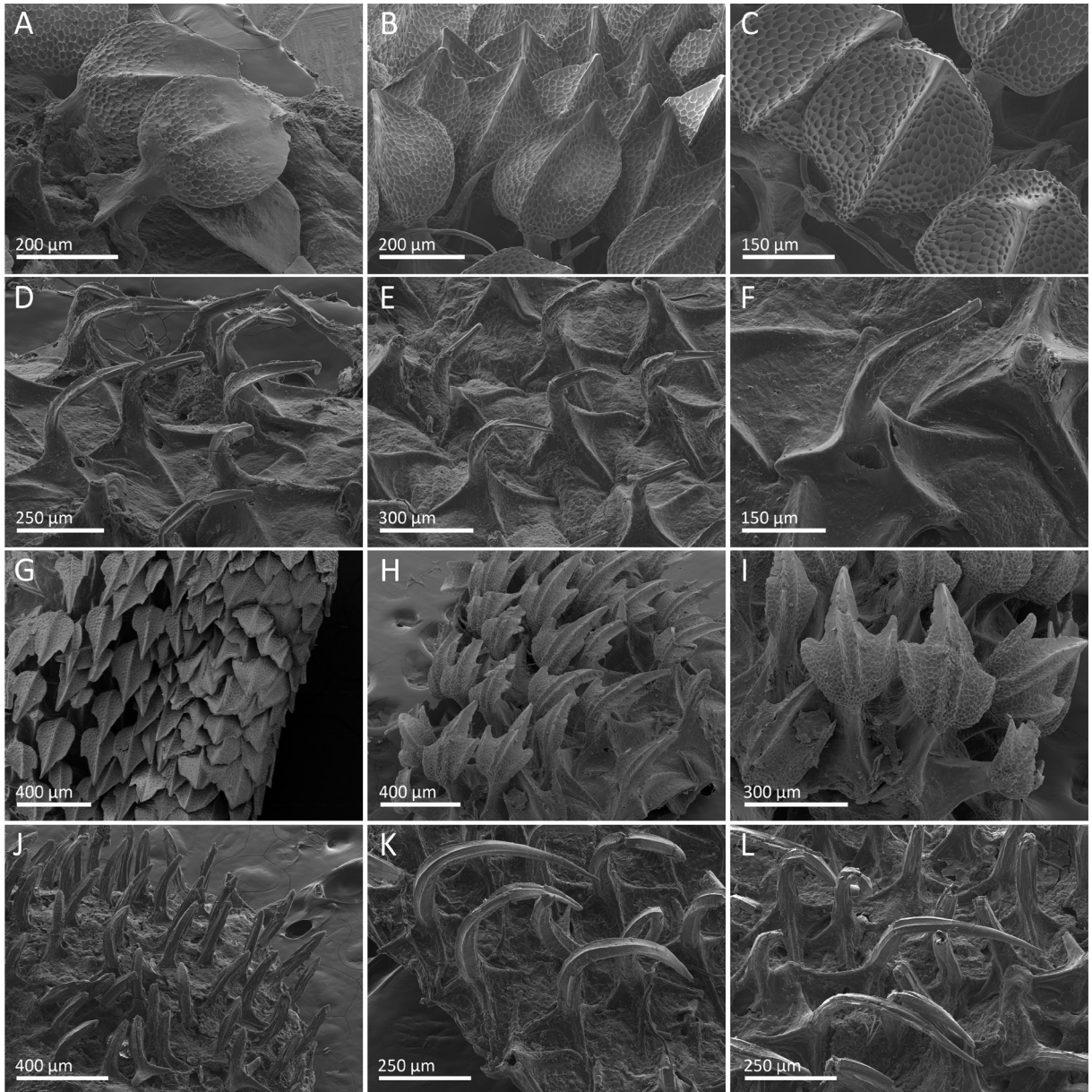


Figure 2. SEM photographs showing details of (A-I) *Apristurus ampliceps* and (J-L) *Etmopterus spinax* squamations. A-C, M1 dermal denticles located on the snout; D-E, M2 dermal denticles located on the dorso-lateral and ventral surface of the body respectively; F, detail of M2 dermal denticle; G, M3 dermal denticles located on the pectoral fin leading edge; H-I, M4 dermal denticles located on the upper margin of the caudal fin; J, M1 dermal denticles located on the snout; K-L, M2 dermal denticles located on the dorso-lateral and ventral surface of the body respectively. Photographs A, E and H-I were taken on specimen I.24355.002/1; photographs B-D and F-G were taken on specimen I.24355-007; and photographs J-L were taken on specimen I.30731-001.

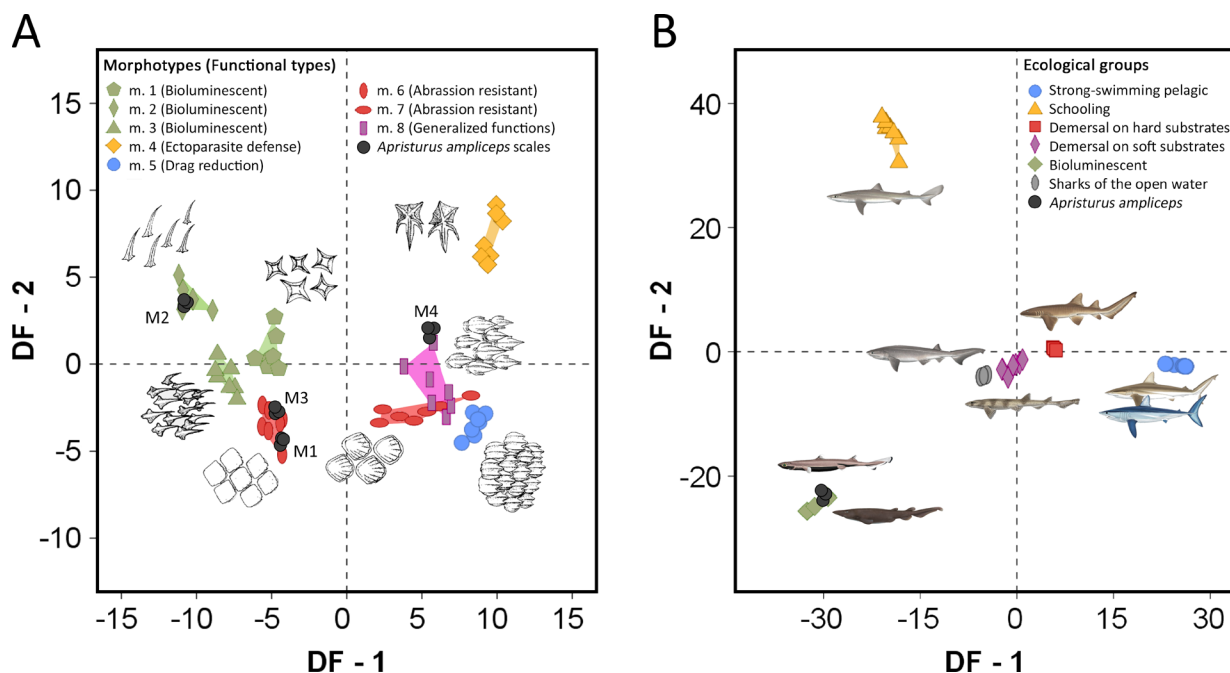


Figure 3. Canonical Variate Analyses results showing the discriminant punctuations of *Apristurus ampliceps* dermal denticles and specimens. A, Canonical Variate Analysis-1 (CVA-1) taking eight dermal denticle morphotypes (m. 1-m. 8, corresponding to five functional types) as defined groups and ten size-free variables of the crown surface as discriminant variables. M1-M4 denote the different dermal denticle morphologies of *A. ampliceps*. B, Canonical Variate Analysis-2 (CVA-2) taking six ecological groups of sharks as defined groups and percentages of coverage of each dermal denticle morphotype used as discriminant variables. Results are plotted based on the first two discriminant functions (DF). Figure modified from Ferrón and Botella (2017).

Bristle-shaped dermal denticles have also been described in *A. profundorum* (Rodríguez-Cabello *et al.*, 2014: Figure 4) and *A. manis* (Springer, 1979: Figure 62) which, together with *A. ampliceps*, constitute a monophyletic group according to molecular data (Naylor, *et al.*, 2012). In contrast, the typical morphology of the dorso-lateral dermal denticles of all other *Apristurus* species examined so far differs substantially from that of the bristle-shaped dermal denticles described here for *A. ampliceps*, showing tricuspid crowns with well-developed ridges and usually denser distributions (Springer, 1979: Figure 8; Compagno, 1984; Nakaya and Séret, 1999: Figure 2; Sato *et al.*, 1999: Figure 2; 2008: Figure 5; 2013: Figure 10; Iglésias *et al.*, 2004: Figure 2; Kawauchi *et al.*, 2008: Figure 3 and 11; Nakaya *et al.*, 2008: Figure 4; White *et al.*, 2008: Figure 2; Castro 2010: Figure 68-71, 73-74 and 76; Iglésias 2012: Figure 3). This was corroborated first-hand in other seven *Apristurus* species deposited in the Australian Museum (*A. australis*, I. 15973-004; *A. harrisoni*, I. 25853-011; *A. herklotsi*, I. 42760-002; *A. melanoasper*, I. 24058-007; *A. pinguis*, I. 25095.006/2; *A. platyrhynchus*, I. 28067-015; *A. sinensis*, I. 24462-005 30F4). In fact,

according to Ferrón and Botella's (2017) analyses, the predominant dermal denticle morphologies in *A. nasutus*, *A. canutus* and *A. parvipinnis* are more similar to those of dermal denticles with generalized functions and the squamation pattern of those sharks is typical of non-bioluminescent open-water species. On the other hand, it is possible to recognize common traits in the squamation of *A. ampliceps* and all the other congeneric species including a similar crown morphology and density of the dermal denticles located on the snout and the fin leading edges, the generalized presence of honeycomb-like ornamentation and the absence of dorso-ventral differentiation (but see Taylor, 1972).

Our results further support the presence of ontogenetic change in the squamation of *A. ampliceps*. Comparison with the squamation of a mature specimen (82.6 cm) described by Sasahara *et al.* (2008) reveals two main differences between juvenile and adult specimens: (1) juveniles have some rows of large tricuspid dermal denticles in the leading edge of the caudal fin (although not forming a well-developed crest as in other *Apristurus* species) (Figure 1A and Figure 2H-I), which are absent in adults (Sasahara *et al.*, 2008);

and (2) dermal denticles on the dorso-lateral region of the body are slender in juveniles and more leaf-like in adults (compare Figure 2D-F with Sasahara *et al.*, 2008: Figure 4). The latter ontogenetic pattern could be widespread among deep water scyliorhinid sharks as it has also been noticed in *Galeus piperatus* (Hubbs and Taylor, 1969), *A. kampae* (Taylor, 1972), *A. melanoasper* and *A. laurussonii* (Iglésias *et al.*, 2004), and could be present in the other two *Apristurus* species with bristle-shaped dermal denticles (i.e. *A. profundorum* and *A. manis*) (note more robust adult dermal denticles in Castro, 2010: Figure 72 and 75). The existence of spatial segregation of juveniles and adults in *Apristurus* species entails significant habitat shifts through their lifetime (Flammang *et al.*, 2011) which could account for the ontogenetic variation of their squamation as it has also been documented in another shark species (i.e. *Galeorhinus galeus* in Ferrón and Botella, 2017). These ontogenetic shifts might, however, not necessarily entail the loss of bioluminescence, as some etmopterids with similar ontogenetic patterns (Coelho *et al.*, 2018) do not undergo notable variations on their light emission capability (Reif, 1985a; Claes and Mallefet, 2009a). In any case, a detailed study on mature specimens of *A. ampliceps* is needed to determine whether the squamation pattern of adults is also consistent with the existence of bioluminescence at that stage.

The existence of typical bioluminescent squamation patterns in *A. ampliceps* juveniles has several different implications. Firstly, this finding suggests that bioluminescence might have evolved several times among phylogenetically distantly related shark taxa, being more widespread than previously thought for this group. Secondly, if confirmed, this would constitute the first record of bioluminescence within the Superorder Galeomorpii, contributing to the advance of knowledge on the ecological diversity of deep-water scyliorhinid and carcharhiniform sharks. Finally, the discovery of bioluminescence in non-squalomorph groups could provide an independent scenario for testing previously proposed hypotheses about functionality and ecological relevance of bioluminescence in sharks (e.g. Reif, 1985a; Claes and Mallefet, 2008, 2009a, b; Claes *et al.*, 2015). From this promising perspective, we recommend the quantitative study of the squamation patterns of other deep-water galeomorphs showing similar bristle-like dermal denticles, such as *A. profundorum* (Rodríguez-Cabello *et al.*, 2014: Figure 4), *A. manis* (Springer, 1979: Figure 62) and *Cephalurus cephalus* (Castro, 2010: Figure 79), as well as the search for bioluminescent organs in freshly caught specimens.

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Online supplementary information

Table S1. Dermal denticle morphotypes and functional types considered in Ferrón and Botella (2017) and their occurrences in the different ecological groups.

Table S2. Numerical values for discriminant variables measured on *Apristurus amplexus* dermal denticles and detailed results of their classification into dermal denticle morphotypes and functional types after their inclusion in Canonical Variate Analysis-1 (CVA-1) performed by Ferrón and Botella (2017).

Table S3. Percentage of coverage of each functional type and morphotype in all studied specimens of *Apristurus amplexus* and detailed results of their classification into predefined ecological groups after their inclusion in Canonical Variate Analyzes-2 (CVA-2) performed by Ferrón and Botella (2017).