



Illuminating the evolution of bioluminescence in sharks

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Typescript received 17 October 2022; accepted in revised form 26 January 2023

Abstract: The evolutionary context in which shark bioluminescence originated is poorly understood, despite it being critical to uncovering influential factors in the evolutionary history and diversity of living chondrichthyans as well as the mechanisms of deep-water colonization by vertebrates. This study provides the first joint reconstruction of the habitats, lifestyles, and occurrence of bioluminescence in the evolution of squalomorph sharks using ancestral state estimation analysis to resolve the timing of deep-sea colonization, the evolutionary origin of bioluminescence and the ancestral ecologies of this group. The results suggest that most squalomorphs originated in neritic environments from where they colonized deep waters on several independent occasions during the Late Jurassic and Early Cretaceous, predating most of the

previous estimates of the timing of this event. The colonization of the deep sea took place via the benthic zone, in contrast to the view that an intermediate mesopelagic stage occurred during this ecological transition. Finally, the analyses accounting for uncertainty of the presence of bioluminescence strongly support that this trait evolved only once among sharks in a bathydemersal ancestor. This study reveals that shark bioluminescence evolved in a complex scenario that combines elements of several previous proposals, and enriches our perspective on the sequence of events that characterized the vertebrate conquest of the deep sea.

Key words: shark, bioluminescence, deep-sea colonization, ancestral state estimation.

BIOLUMINESCENCE is a phenomenon of great significance in aquatic communities and a major component in the shaping of deep-sea ecosystem dynamics (Haddock *et al.* 2010). This adaptation is widespread among marine organisms, and is involved in essential functions related to camouflage, defence, predation and communication (Widder 2010; Davis *et al.* 2016). In sharks, the presence of bioluminescence has been unambiguously proven in representatives of three different families of the order Squaliformes: Etmopteridae, Dalatiidae and Somniosidae (Straube *et al.* 2015; Duchatelet *et al.* 2021a, 2021b); all of them are deep water taxa inhabiting mostly mesopelagic environments, continental slopes and abyssal plains (Ebert *et al.* 2021). Most of the research carried out on the bioluminescence of these groups has focused on aspects related to the histology, physiological basis and underlying control mechanisms of the photogenic organs (Claes & Mallefet 2009a, 2010a, 2010b, 2011, 2015; Claes *et al.* 2010a, 2011a, 2011b, 2012; Renwart 2013; Renwart & Mallefet 2013; Renwart *et al.* 2015; Duchatelet *et al.* 2019a, 2019b, 2020a, 2020b, 2020c; Delroisse *et al.* 2021; Mallefet *et al.* 2021; Mizuno *et al.* 2021), photophore distribution and its interrelationship with squamation patterns (Hubbs *et al.* 1967; Reif 1985; Claes & Mallefet 2009b; Claes *et al.* 2014a; Ferrón & Botella 2017;

Ferrón *et al.* 2018; Mallefet *et al.* 2021; Lourtie *et al.* 2022), embryology and ontogeny (Claes & Mallefet 2008, 2009c; Duchatelet *et al.* 2019c; Van den Bossche 2020) and function in living forms (Reif 1985; Munk & Jørgensen 1988; Widder 1998; Claes & Mallefet 2009b; Claes *et al.* 2010b, 2013, 2014b, 2014c, 2020; Duchatelet *et al.* 2019d; Mallefet *et al.* 2021). However, a deep-time perspective on the scenario in which bioluminescence evolved is lacking, despite it being crucial to identifying factors significant for the evolutionary history and diversity of living chondrichthyans as well as to shedding light on the mechanisms of deep-water colonization by sharks and vertebrates in general.

Two main competing hypotheses have been proposed to explain the circumstances that contributed to the evolution of bioluminescence and its involvement in the colonization of deep-sea environments by sharks, herein referred as the 'deep-to-shallow' and 'shallow-to-deep' scenarios. The 'deep-to-shallow' hypothesis (Adnet & Cappetta 2001; Claes & Mallefet 2009b) postulates that the emergence of ecological opportunity after the extinction of several benthic deep-water forms during the Cenomanian–Turonian global anoxic event (*c.* 90 Ma) promoted the colonization of empty deep-water niches by etmopterids, somniosids, and other demersal non-bioluminescent squaliform

relatives (e.g. Centrophoridae and Oxynotidae). Later, the disappearance of several epipelagic predaceous forms during the Cretaceous–Palaeogene mass extinction enabled secondary integration of dalatiids into shallower mesopelagic environments of the Palaeocene. Within this scenario, bioluminescence would have originated in deep waters, most likely in the aphotic realm, with a presumed function in intraspecific signalling that later became an exaptation as counterillumination in mesopelagic forms. On the other hand, the more recently proposed ‘shallow-to-deep’ hypothesis (Klug & Kriwet 2010; Claes *et al.* 2012, 2014b; Flammensbeck *et al.* 2018; Duchatelet *et al.* 2021a) claims that bioluminescence first evolved as a counterillumination camouflage adaptation in the photic zone and later enabled etmopterids to colonize deep-water habitats by aiding intraspecific signalling mechanisms and promoting rapid diversification of this group in aphotic ecosystems (Straube *et al.* 2010; Claes *et al.* 2015). This discussion is further obscured by the still unresolved debate on the single (Klug & Kriwet 2010; Claes *et al.* 2012, 2014b; Straube *et al.* 2015; Duchatelet *et al.* 2021a) versus double (Hubbs *et al.* 1967; Reif 1985; Claes & Mallefet 2009b; Straube *et al.* 2010) evolutionary origin of bioluminescence in sharks.

The elucidation of the context in which this trait evolved relies then on the application of holistic approaches to simultaneously resolve the timing and tempo of deep-sea colonization, the evolutionary origin of bioluminescence and the ancestral ecology of bioluminescent groups, incorporating evidence from both living and extinct taxa in a phylogenetic and temporal context. With this aim, this study offers for the first time a joint reconstruction of the habitats, lifestyles, and occurrence of bioluminescence in the evolutionary history of the superorder Squalomorphii by integrating comparative phylogenetic methods with sedimentological and taphonomic information on fossil occurrence and the autecology of living species.

MATERIAL AND METHOD

A dataset was generated including habitats (i.e. neritic, bathyal and abyssal realms), lifestyles (i.e. demersal, benthopelagic and pelagic) and the presence of bioluminescence in squaliform sharks (and closely related groups of squalomorphs), containing 23 living and 61 fossil taxa (Table S1). The dataset includes: 5 living and 12 fossil Somniosidae; 1 living and 1 fossil Oxynotidae; 5 living and 8 fossil Etmopteridae; 4 living and 11 fossil Dalatiidae; 2 living and 6 fossil Centrophoridae; 2 living and 6 fossil Squalidae; 1 living and 4 fossil Squatiniformes (plus 5 *Protospinax* spp.); 2 living and 2 fossil Pristiophoriformes; and 1 living and 6 fossil Echinorhiniformes. Currently, the number of described living species in each of these groups is: 16 in

Somniosidae, 5 in Oxynotidae, 51 in Etmopteridae, 9 in Dalatiidae, 16 in Centrophoridae, 37 in Squalidae, 22 in Squatiniformes, 10 in Pristiophoriformes, and 2 in Echinorhiniformes (Ebert *et al.* 2021). Probabilities (from 0 to 1) were assigned to each character state in the tips based on different criteria (see below).

Ancestral character state estimation was performed by implementing stochastic character mapping with the *make.simmap()* function in the phytools package (Revell 2012) in R (v.4.0.0; R Core Team 2013), after tree manipulation with the R packages ape (Paradis & Schliep 2019), dispRity (Guillerme 2018), tidytree (Yu 2022), and treeio (Wang *et al.* 2020). A total of 1000 simulated stochastic character histories were obtained for each character using the tip states on the tree and a continuous-time reversible Markov model of trait evolution, fitted on the phylogenetic hypothesis from Flammensbeck *et al.* (2018).

This choice is justified because this constitutes the most recent and complete time-calibrated total-evidence phylogeny of squalomorph sharks (based on tooth morphology and concatenated exon sequences) including both living and fossil representatives and representing a more integrative framework than previous purely molecular phylogenies (Straube *et al.* 2010, 2015). Hypotheses based on morphological characters other than teeth (Shirai 1992, 1996; Carvalho 1996; Carvalho & Maisey 1996) are not considered here because they have been rejected later by different lines of evidence from the fossil record (Kriwet *et al.* 2009; Klug & Kriwet 2013) and molecular data (Douady *et al.* 2003; Winchell *et al.* 2004). The 50% majority-rule consensus tree and the mean age estimates of nodes were considered. In order to account for phylogenetic and temporal uncertainty, all the analyses were repeated in a randomly selected sample of 1000 phylogenies from the posterior tree distribution, representing unique topologies and time calibrations. Nomenclature and taxonomy of extinct taxa follows Flammensbeck *et al.* (2018).

Different models were implemented, including equal rates for all permitted transitions (ER), symmetric backward and forward rates for all permitted transitions (SYM), and all-rates-different for permitted transitions (ARD), and compared using the Akaike criterion. In order to overcome the issue of choosing among alternative models when several of them have comparable support, further analyses were performed generating stochastic maps under all of the competing models, in proportion to the weight of evidence in support of each of them (considering Akaike weights).

For living taxa, the coding of habitats and lifestyles was established based on the ecological and biological information in Ebert *et al.* (2021), Froese & Pauly (2022), and the IUCN (2021) (Text S1). Equal tip state probabilities were coded for more than one habitat state in species that

normally occupy several of the predefined categories. The species typically associated with the bottom and those living in the water column were coded as demersal and pelagic taxa, respectively, whereas primarily demersal species that make incursions into the water column were coded as benthopelagic taxa. Species whose bioluminescence has been proved during *in vivo* observations or by reports of photophores in captured specimens (i.e. all living etmopterids and dalatiids and the somniosid *Zameus squamulosus*) were coded as bioluminescent taxa (Duchatelet *et al.* 2021a and references therein). Equal tip state probabilities were considered for both the presence and absence of bioluminescence in the rest of the living species of the Somniosidae + Oxynotidae clade as data on the biology of these elusive deep-water sharks are especially scarce and the question of whether or not bioluminescence is a shared trait among all somniosids remains unresolved (Hubbs *et al.* 1967; Straube *et al.* 2015; Duchatelet *et al.* 2021a). This procedure relaxed the assumptions that would have largely been based on the absence of evidence and allowed the analysis to accommodate this uncertainty in the ancestral states (Bollback 2006).

For extinct taxa, the coding of habitat was informed by sedimentological, palaeobathymetrical and taphonomical data from the literature (see Text S1). Uncertainty was incorporated by considering equal tip state probabilities for certain habitats in taxa for which: (1) multiple records were associated with different habitat categories; (2) the information available was not complete enough to further refine the palaeoenvironmental/palaeobathymetrical inferences; or (3) competing palaeoenvironmental/palaeobathymetrical hypotheses existed for the same fossil sites. Lifestyle and the presence of bioluminescence were coded as uncertain, with equal probabilities for all tip states.

Four additional analyses were performed with modified character codings considering: (1) all living species in the Oxynotidae clade as non-bioluminescent taxa (Table S1, Oxynotidae); (2) all living species in the Somniosidae + Oxynotidae clade (except *Zameus squamulosus*) as non-bioluminescent taxa (Table S1, Somniosidae); (3) only shallow water (= neritic realm) and deep-water (= bathyal and abyssal realms) character states for habitat; and (4) only demersal and pelagic character states for lifestyle. In the last case, both states were given equal probabilities for the species coded as benthopelagic taxa in the original analysis (Table S1).

RESULTS

Character transition models with the highest support (i.e. highest AIC weights) are ARD and SYM in the analyses of habitat, ER and SYM in the analyses of lifestyle, and ER in the analyses of bioluminescence (Fig. 1). Results presented in the main text correspond to those derived from integrating stochastic character maps across multiple character transition models in proportion to their AIC weights.

The last common ancestor (LCA) of the Echinorhinoformes + Pristiophoriformes + Squatiniformes + Squaliformes clade (node 1) was reconstructed as a non-bioluminescent benthic shark in the neritic realm (corresponding to the character states with the highest probabilities; Fig. 2). From this condition, deep-water habitats of the bathyal realm were colonized independently by the LCAs of the Centrophoridae + Dalatiidae + Etmopteridae + Somniosidae clade in the Late Jurassic (c. 150 Ma) (node 3) and Pristiophoriformes (after

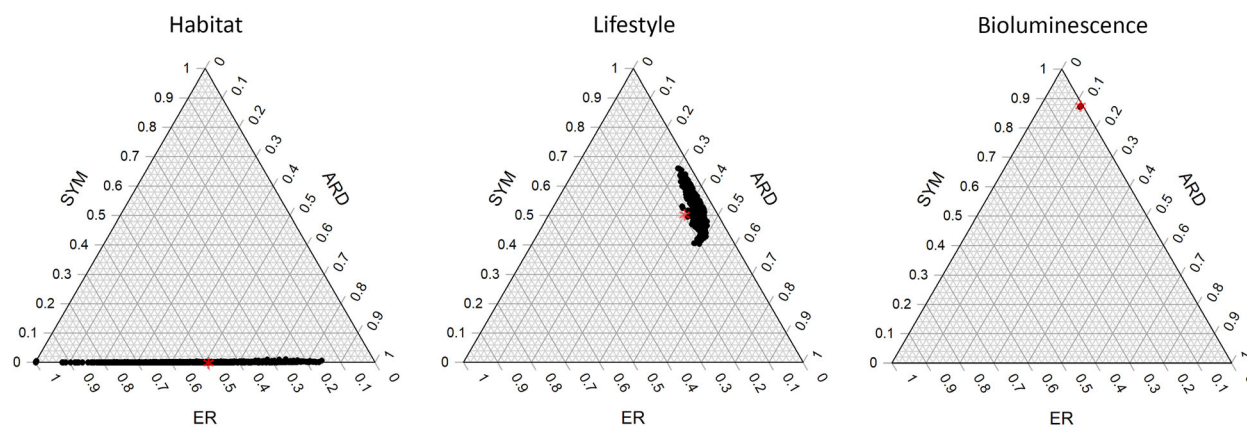


FIG. 1. Ternary plots showing Akaike information criterion (AIC) weights of each character transition model (ER, equal rates; SYM, symmetrical rates; and ARD, all rates different) for the different analysed traits (habitat, lifestyle and occurrence of bioluminescence). Red asterisks represent data from the 50% majority-rule consensus tree with mean age estimates of nodes from Flammensbeck *et al.* (2018) and black dots represent data from the sample of 1000 phylogenies from the posterior tree distribution.

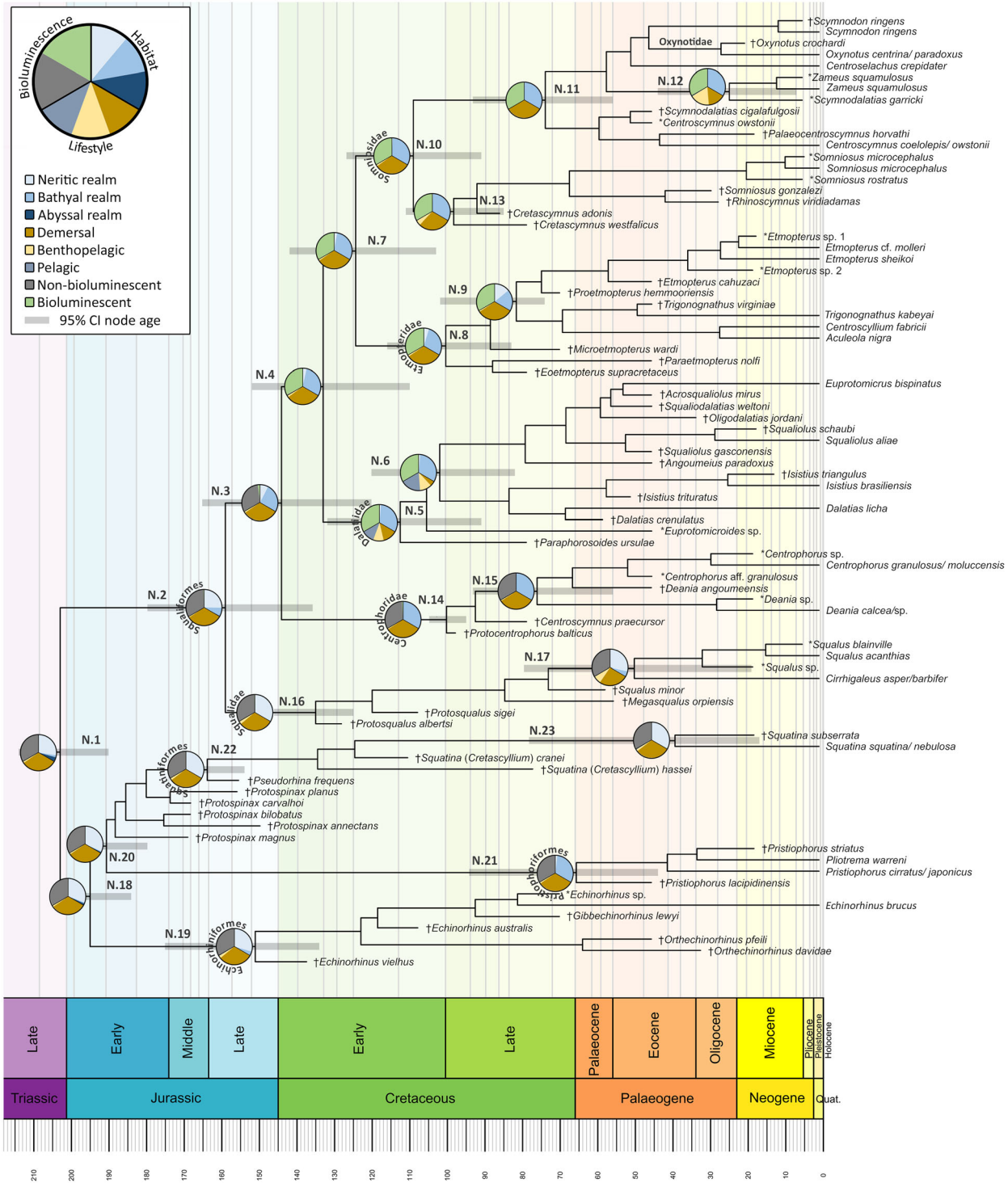


FIG. 2. Ancestral state estimation of the habitats, lifestyles, and occurrence of bioluminescence in the squalomorph phylogeny integrating stochastic character maps across multiple character transition models (ER, SYM and ARD). Pie charts show character-state probabilities in the main nodes. Grey bars show 95% confidence intervals of node ages. The phylogeny corresponds to the 50% majority-rule consensus tree with mean age estimates of nodes from Flammensbeck *et al.* (2018). Extinct taxa are marked with a dagger (†), while fossil taxa which are assigned to extant taxa, are marked with an asterisk (*).

node 20, in the branch leading to node 21) around the Jurassic–Cretaceous boundary (*c.* 145 Ma), Squaliformes (between nodes 16 and 17) in the Late Cretaceous (*c.* 90 Ma) and Echinorhiniformes (after node 19) in the Late Cretaceous and Palaeogene (*c.* 90 Ma and 30 Ma, respectively) (Fig. 2; Fig. S1). A demersal lifestyle was predicted for most of the ancestral nodes of squalomorph sharks. From this condition, pelagic and benthopelagic lifestyles evolved within the Dalatiidae (node 6) and Somniosidae (node 12) close to the Early–Late Cretaceous boundary (*c.* 100 Ma) and the Palaeogene–Neogene boundary (*c.* 23 Ma), respectively (Fig. 2; Fig. S2). Finally, bioluminescence was predicted to have evolved only once in the LCA of the Dalatiidae + Etmopteridae + Somniosidae clade (node 4) during the Early Cretaceous (*c.* 130 Ma). The analysis predicted that the LCA of all bioluminescent species was a demersal shark living in the bathyal realm (Fig. 2). This result was also supported when the living species in the Oxynotidae clade were considered as non-bioluminescent taxa ('Oxy' column in Fig. 3; Fig. S3). The more constrained analysis assuming all somniosid species, except *Zameus squamulosus*, as non-bioluminescent sharks supported a triple origin of bioluminescence, with this trait evolving independently in the LCAs of the Dalatiidae and Etmopteridae (nodes 5 and 9) in the Early Cretaceous (*c.* 115 Ma) and the Early–Late Cretaceous boundary (*c.* 100 Ma), respectively, and within the Somniosidae in the LCA of the *Zameus* + *Scymnodalatis* clade (node 12) close to the Palaeogene–Neogene boundary (*c.* 23 Ma; 'Som' column in Fig. 3; Fig. S4). The analyses accounting for temporal and phylogenetic uncertainty recover virtually the same evolutionary patterns (Fig. 4), suggesting that the impact of these potential biases is negligible.

Detailed results of the analyses considering only a single transition model can be found in Figures S5–S11 (for ER), Figures S12–S18 (for SYM) and Figures S19–S25 (for ARD).

DISCUSSION

The colonization of the deep sea predates previous estimates

The results of this study reinforce the idea that squaliforms, and most other orders of squalomorphs, originated and diversified in neritic shallow waters (Adnet & Cappetta 2001). It is most likely that colonization of bathyal deep-water environments took place in the Late Jurassic (Figs 2–4; Fig. S1), far predating previous proposals for this ecological shift (Early Cretaceous in Adnet & Cappetta 2001; Early Cretaceous in Claes & Mallefet 2009b; Late Cretaceous in Kriwet & Klug 2009; Early/Late Cretaceous boundary in Klug & Kriwet 2010; Cretaceous/Tertiary boundary in Straube *et al.* 2010) and suggesting that

the Cenomanian–Turonian global anoxic event and the Cretaceous–Palaeogene mass extinction played secondary roles, if any at all, in this transition. In contrast, the Late Jurassic to Early Cretaceous shelf dysoxic–anoxic event (Nozaki *et al.* 2013; Rogov *et al.* 2020) represents a more plausible abiotic trigger in this context; it might have created new empty niches and favourable conditions in the bathyal realm that facilitated the occupation of these habitats by demersal squalomorph sharks. In fact, continental slopes were also presumably colonized by other squalomorph groups on at least five additional independent occasions, by pristiophoriforms, squaliforms and echinorhiniforms (Figs 2–4; Fig. S1), supporting the hypothesis that ancestrally neritic squalomorphs might already have possessed a suite of pre-adaptations that predisposed them to occupy this kind of environment when the ecological opportunity arose. These patterns are also supported when considering only two character states (shallow and deep water; 'Hab' column in Figs 3, 4; Fig. S1). In any case, these results should be interpreted with caution given the scarcity of deep-water deposits (Kriwet & Klug 2009; Klug & Kriwet 2010) and, as a consequence, the hypothesis that these squalomorph groups were ancestrally adapted to living in bathyal habitats cannot be fully rejected (Sorenson *et al.* 2014). However, incorporation of fossil information in macroevolutionary inference usually leads to improved estimation of ancestral states (Oakley & Cunningham 2000; Finarelli & Flynn 2006; Albert *et al.* 2009; Slater *et al.* 2012; Betancur-R *et al.* 2015), even when an important part of these data is biased or incorrect (Puttick 2016).

The colonization of the deep sea took place via the benthic realm

Ancestral state estimation analysis also revealed that most squalomorph orders originated as demersal forms and only dalatiids and some somniosids ancestrally displayed pelagic and benthopelagic lifestyles, respectively (Figs 2–4). A fully pelagic lifestyle was also supported as the ancestral condition of the dalatiids when considering only two character states (benthic and pelagic; 'Lif' column in Figs 3, 4; Fig. S2). These results indicate that colonization of deep-water habitats occurred via the benthic zone and that dalatiids integrated secondarily into the water column, in agreement with, but much earlier than, the process proposed by Adnet & Cappetta (2001) and Claes & Mallefet (2009b). This contrasts with the view that the acquisition of a mesopelagic lifestyle (exemplified by dalatiid sharks) constituted an intermediate step in the colonization of deep-water habitats by squaliforms (Klug & Kriwet 2010; Claes *et al.* 2012, 2014b; Flammensbeck *et al.* 2018; Duchatelet *et al.* 2021a).

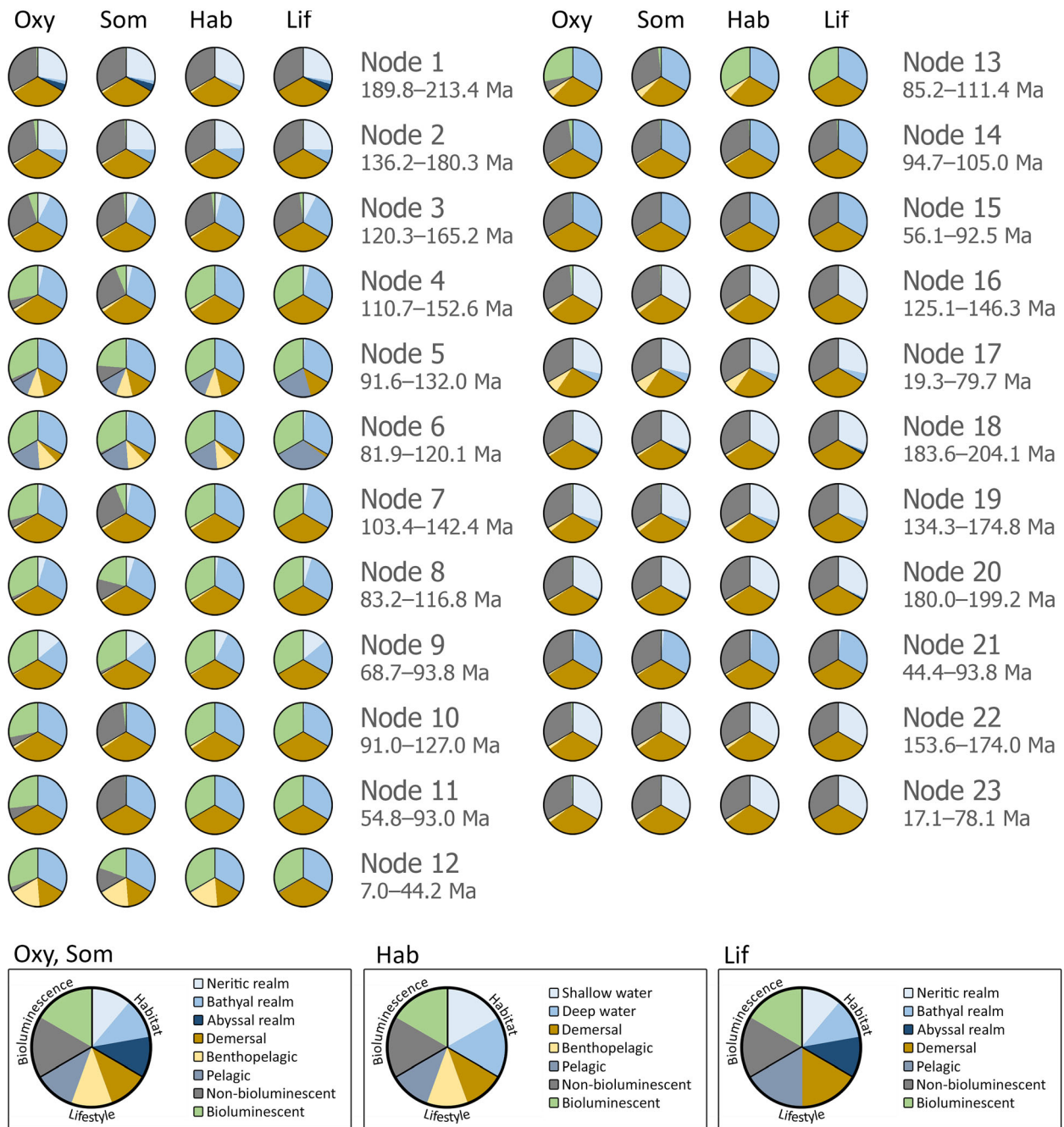


FIG. 3. Ancestral state estimation of the habitats, lifestyles and occurrence of bioluminescence in the squalomorph phylogeny integrating stochastic character maps across multiple character transition models (ER, SYM and ARD) and considering: Oxy, all living species in the Oxynotidae clade as non-bioluminescent taxa; Som, all living species in the Somniosidae + Oxynotidae clade (except *Zameus squamulosus*) as non-bioluminescent taxa; Hab, only shallow water (= neritic realm) and deep-water (= bathyal and abyssal realms) character states for habitat; Lif, only demersal and pelagic character states for lifestyle. Pie charts show probabilities for each character state. Node numbers correspond to those in Figure 2.

Bioluminescence evolved only once among sharks

The results of this study provide consistent evidence for a single origin of bioluminescence in squaliforms. The analyses of the Somniosidae, which incorporated uncertainty,

predicted that this trait was already present in the LCA of the Dalatiidae + Etmopteridae + Somniosidae clade during the Early Cretaceous (*c.* 130 Ma; Figs 2–4), which was still supported when assuming living oxynotids (included here in the same clade as somniosids) to be non-

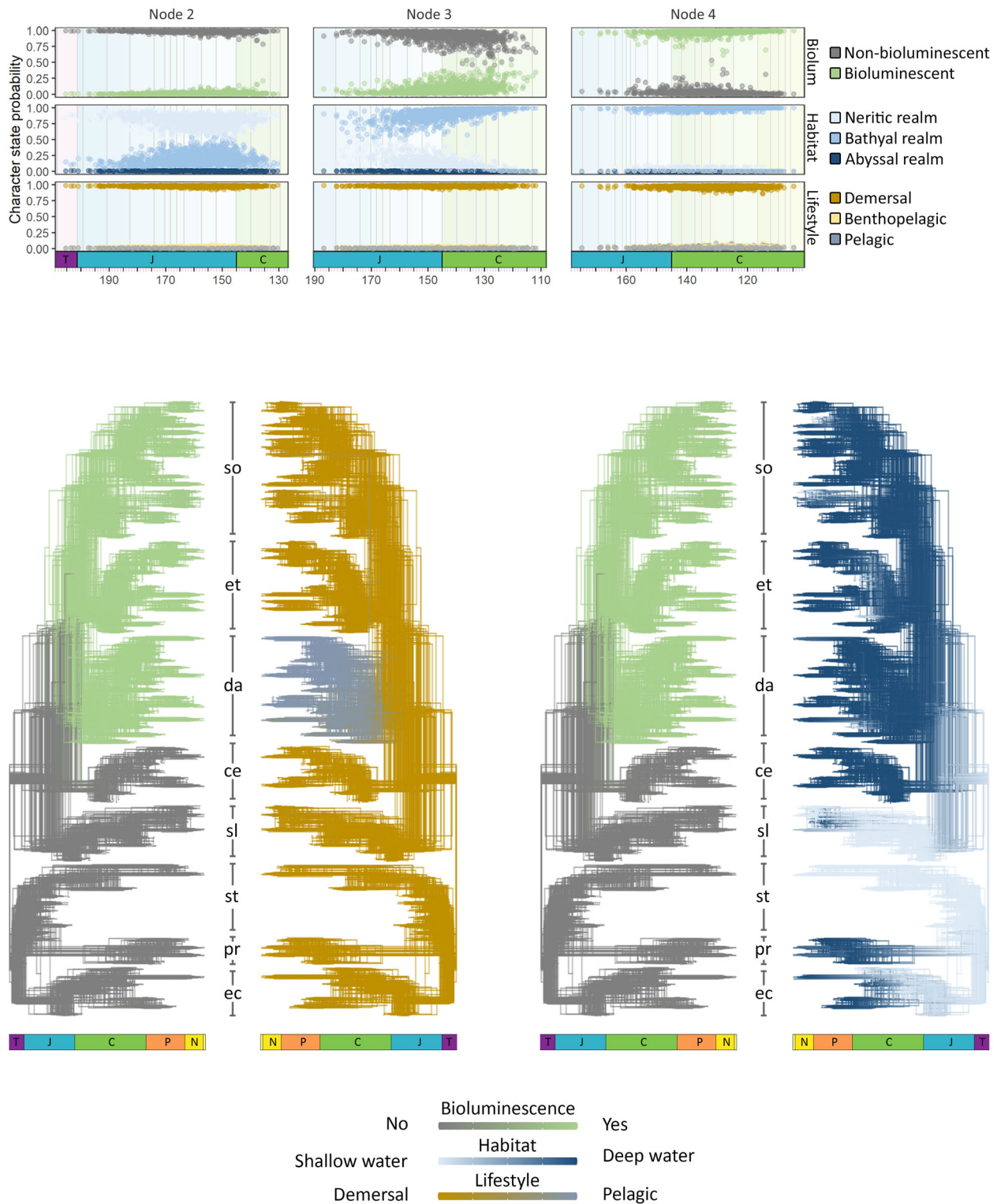


FIG. 4. Ancestral state estimation of the habitats, lifestyles and occurrence of bioluminescence in the squalomorph phylogeny integrating stochastic character maps across multiple character transition models (ER, SYM, and ARD) and accounting for phylogenetic and temporal uncertainty, considering a sample of 1000 phylogenies from the posterior tree distribution from Flammensbeck *et al.* (2018). The upper panels show the age and character state probability of three key nodes in the phylogeny. Node numbers correspond to those in Figure 2. The lower panel includes a randomly selected subsample of 100 phylogenies representing results in density trees. Clades: ce, Centrophoridae; da, Dalatiidae; ec, Echinorhiniformes; et, Etmopteridae; pr, Pristiophoriformes; sl, Squalidae; so, Somniosidae; st, Squatiniformes.

bioluminescent sharks ('Oxy' column in Fig. 3; Fig. S3). On the contrary, a triple independent origin in the Dalatiidae, Etmopteridae and Somniosidae was predicted when all living species in the Somniosidae + Oxynotidae clade, except *Zameus squamulosus*, were considered as non-bioluminescent taxa ('Som' column in Fig. 3; Fig. S4). However, the ecological evidence behind this assumption is weak and this scenario should be regarded as very unlikely given the robust results obtained from the analyses incorporating uncertainty and the strength of the morphological and physiological data favouring homology and a single origin of bioluminescence for relatives of all three families (Claes *et al.* 2012; Duchatelet *et al.* 2020a, 2020b, 2020c, 2021a; Mallefet *et al.* 2021). This pattern contrasts with that found in osteichthyans, the other major group of vertebrates with bioluminescent representatives, in which bioluminescence has independently evolved at least 27 times (Davis *et al.* 2016). The fact that bioluminescence is more conspicuous in osteichthyans than in chondrichthyans may reflect the physiological constraints of the latter, related to their urea-based osmoregulation, high energetic cost of lipid accumulation, and reliance on a nitrogen-rich diet, that hinder the colonization of deep-water habitats where bioluminescence may confer an adaptive advantage (Musick & Cotton 2015; Treberg & Speers-Roesch 2016). However, differences between the two groups are also evident in the broader diversity of the control mechanisms displayed and habitats occupied by bioluminescent osteichthyans (Davis *et al.* 2016).

Implications for the evolutionary scenario underlying the emergence of bioluminescent sharks

The joint reconstruction of the ecological setting in which bioluminescence evolved in sharks supports a complex scenario, combining elements of both 'deep-to-shallow' and 'shallow-to-deep' hypotheses. In all analyses performed, and even when contemplating the improbable scenario of a multiple independent origin, the colonization of deep-water habitats precedes the emergence of bioluminescence (Figs 2–4); thus, this result challenges the presumed role of bioluminescence as a triggering or enabling factor in the early conquest of the bathyal realm by squaliforms (Adnet & Cappetta 2001; Klug & Kriwet 2010; Claes *et al.* 2012; Straube *et al.* 2015; Flammensbeck *et al.* 2018). However, the impact of this adaptation on the posterior diversification and increased rates of evolution of certain deep-sea groups seems clear, especially in those in which bioluminescence fulfils a function in signalling (i.e. in the Etmopteridae) (Straube *et al.* 2010; Claes *et al.* 2015) in analogy with a number of bioluminescent bony fish clades (Davis *et al.* 2016).

The LCA of all bioluminescent sharks is predicted as a demersal form inhabiting the bathyal realm. This finding challenges the commonly accepted view that assumes counterillumination as the ancestral function of shark bioluminescence (Klug & Kriwet 2010; Claes *et al.* 2012, 2014b; Flammensbeck *et al.* 2018; Duchatelet *et al.* 2021a, 2021b), given its limited utility in organisms that mostly live close to the substrate. Instead, other functions related to intraspecific signalling (Reif 1985; Straube *et al.* 2010), predator deterrence (Munk & Jørgensen 1988; Claes *et al.* 2013, 2020; Duchatelet *et al.* 2019d) or prey capture (Widder 1998; Claes & Mallefet 2009b; Claes *et al.* 2010b; Mallefet *et al.* 2021) may be better candidates. Evolutionary, ecological and functional inferences on the last common ancestor of bioluminescent sharks might be benefited from future analyses incorporating information relative to their squamation patterns (Ferrón & Botella 2017; Lourtie *et al.* 2022) and physiology (Claes & Mallefet 2009b; Duchatelet *et al.* 2021b).

This study, based on phylogenetic comparative methods, offers the first comprehensive perspective on the scenario that underlies the deep-sea colonization and emergence of bioluminescent sharks. In a wider context, it enriches our understanding of the mechanisms and patterns that characterize the evolution of this particular adaptation in chondrichthyans and, most importantly, vertebrates as a whole, complementing the body of evidence generated from studies of osteichthyans (Davis *et al.* 2016). Despite being most likely to represent an isolated phylogenetic event, the acquisition of bioluminescence in sharks had important consequences in the evolutionary history of chondrichthyans and enabled the diversification of squaliform groups that nowadays play a fundamental role worldwide as predators in bathyal ecosystems and constitute one of the earliest lineages of vertebrates to glow in the darkness of the Mesozoic deep sea.

CONCLUSIONS

1. Representatives of most squalomorph groups colonized deep waters on several independent occasions during the Late Jurassic and Early Cretaceous.
2. These transitions took place via the benthic zone without an intermediate mesopelagic stage
3. Bioluminescence evolved only once among sharks in a bathydemersal ancestor.

Acknowledgements. I thank the editorial team and three anonymous reviewers for providing thoughtful and valuable comments on the manuscript. This work was supported by the MCIN and the 'European Union NextGenerationEU' (grant number RYC2021-032775-I).

DATA ARCHIVING STATEMENT

Data for this study (including R code and associated files) are available in the figshare database: <https://doi.org/10.6084/m9.figshare.16763449>

Editor. Gustavo Ballen

SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1111/pala.12641>):

Appendix S1. Supporting information including Figures S1–S25, Table S1 and Text S1.

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