BIOLOGICAL REVIEWS
Cambridge Philosophical Society
Check for updates
Biol. Rev. (2024), pp. 000–000.
doi: 10.1111/brv.13093

The language of light: a review of bioluminescence in deep-sea decapod shrimps

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ABSTRACT

In the dark, expansive habitat of the deep sea, the production of light through bioluminescence is commonly used among a wide range of taxa. In decapod crustaceans, bioluminescence is only known in shrimps (Dendrobranchiata and Caridea) and may occur in different modes, including luminous secretions that are used to deter predators and/or from specialised light organs called photophores that function by providing camouflage against downwelling light. Photophores exhibit an extensive amount of morphological variation across decapod families: they may be internal (of hepatic origin) or embedded in surface tissues (dermal), and may possess an external lens, suggesting independent origins and multiple functions. Within Dendrobranchiata, we report bioluminescence in Sergestidae, Aristeidae, and Solenoceridae, and speculate that it may also be found in Acetidae, Luciferidae, Sicyonellidae, Benthesicymidae, and Penaeidae. Within Caridea, we report bioluminescence in Acanthephyridae, Oplophoridae, Pandalidae, and new observations for Pasiphaeidae. This comprehensive review includes historic taxonomic literature and recent studies investigating bioluminescence in all midwater and deep benthic shrimp families. Overall, we report known or suspected bioluminescence in 157 species across 12 families of decapod shrimps, increasing previous records of bioluminescent species by 65%. Mounting evidence from personal observations and the literature allow us to speculate the presence of light organs in several families thought to lack bioluminescence, making this phenomenon much more common than previously reported. We provide a detailed discussion of light organ morphology and function within each group and indicate future directions that will contribute to a better understanding of how deep-sea decapods use the language of light.

Key words: bioluminescence, crustacean, decapod, deep sea, light organs, photophore, shrimp.

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I. INTRODUCTION

(1) Light in the ocean

The ocean is the largest ecosystem on Earth, comprising over 99% of all habitable space on the planet, of which most is dark, expansive, and structured only by chemical and physical properties of the water column (Dawson, 2012). The deep sea begins in waters 200–1000 m in depth, known as the mesopelagic or twilight zone (see Table 1 for glossary). The twilight zone is an extremely light-limited environment, as downwelling sunlight attenuates rapidly with depth (Clarke, 1963). Waters below 1000 m are referred to as the bathypelagic or midnight zone due to the complete absence of downwelling sunlight (Koppelmann & Frost, 2008). Survival in the deep sea has resulted in the evolution of a suite of morphological features, for example, the ability to produce light through a process called bioluminescence. This chemical reaction involves the oxidation of a light-emitting molecule, known as luciferin, and a catalytic enzyme called luciferase or, in some cases, a photoprotein (Haddock, Moline & Case, 2010). This reaction typically produces blue light, although violet, green, yellow, orange, and even red bioluminescence have been reported across various taxa (Nicol, 1958; Mensinger & Case, 1992; Herring & Cope, 2005; Johnsen, 2005; Widder, 2010). Bioluminescence has recently been estimated to have 94 independent evolutionary origins across the tree of life (Lau & Oakley, 2021), and it is considered the 'language of light' for many deep-sea organisms, where 'language' here represents a broad message, such as signalling or camouflage.

(2) Marine bioluminescence

Deep-sea animals can utilise extrinsic bioluminescence by harbouring symbiotic bioluminescent bacteria within specialised tissues (Widder, 2010; Duchatelet *et al.*, 2019) or can produce bioluminescence intrinsically through luminous secretions or specialised light organs (Fig. 1). These light organs may be found embedded in the outermost tissues of the body, or internally, as an extension of the hepatopancreas (a glandular structure involved in digestive functions) (Herring, 1985, 2007; Haddock *et al.*, 2010). In the ocean, the language of light is used by animals in a variety of ways, both defensively and offensively (see Widder, 2010; Haddock *et al.*, 2010). Luminous secretions occur when a specialised hepatic product is regurgitated from the mouth or specialised gland to create a luminous cloud (Fig. 1D). This defence mechanism is used to distract dark-adapted predators with light, potentially providing a chance for the animal to escape (Herring, 1985). The use of bioluminescence for counterillumination is probably the most familiar defensive strategy used by species that inhabit the mesopelagic zone. In counterillumination camouflage, also known simply as counterillumination, an animal matches the intensity of its own bioluminescent emissions to that of downwelling sunlight using specialised light organs called photophores (Haddock *et al.*, 2010). These light organs are commonly located along the ventral and lateral sides

Table 1. Glossary.

Bathypelagic	Open water habitat spanning 1000–4000 m in depth.
Benthopelagic	The habitat including the seafloor and the water column above; associated with sea mounts, slopes, and shelves. In some cases, this term may be used to describe animals that inhabit waters near the seafloor and within the water column (up to ∼100 m from the seafloor) at different times of day.
Bioluminescence	Production of light in or by living organisms.
Deep benthic	Seafloor environment in waters with a depth of 200 m or greater.
Diel vertical migration (DVM)	A daily behaviour in which animals migrate to shallow waters at night to feed and find mates before returning to the depths during the day.
Epipelagic	Open water habitat spanning 0–200 m in depth.
Mesopelagic	Open water habitat spanning 200–1000 m in depth.
Organs of Pesta	Internal light organs derived from the hepatopancreas in sergestid shrimps comprised of anterior, mesial, and posterior lobes.
Pelagic	Open water/water column environment.
Photophore	Light-producing organs, consisting of one or more photocytes, one or more lenses, and reflective and optical structures, often used in counterillumination.

of an animal's body (Fig. 1E, F), allowing the disruption of their silhouette from the viewpoint of a predator beneath them (Clarke, 1963).

Photophores are composite organs in which one or more light-emitting cells, called photocytes, are associated with accessory features such as optical structures that may modify the direction, intensity, spectral distribution and/or angular distribution of the emitted light (Nowel, Shelton & Herring, 1998; Bracken-Grissom *et al.*, 2020). Accessory components include refractive, reflective, optical, and light-shielding structures (Nowel *et al.*, 1998). Photophores found along an animal's body may comprise several subunits, each containing at least one photocyte, or they may be located internally, and in some cases, these internal organs may be referred to more specifically (e.g. the organs of Pesta in Sergestidae, see Section II.1.*c*) (Foxton, 1972; Nowel *et al.*, 1998) (Fig. 1A–C).

External, or dermal, photophores are often cup-shaped organs embedded within the surface tissues along the ventral and lateral sides of an animal's body (Clarke, 1963). The open end of the photophore may contain one or more lenses (when they are referred to as 'lensed photophores'), while the inner surface is typically lined with a reflective layer (Clarke, 1963). The morphology of lensed photophores is highly variable among taxa (see Fig. 2 for examples of photophore structure in decapod shrimps). In some taxa, light emitted from photophores has been experimentally shown to match precisely the intensity of downwelling light, and therefore a function in camouflage is likely (Warner, Latz & Case, 1979; Davis *et al.*, 2020). Counterillumination is known to occur in many pelagic animals including several non-insect pancrustaceans (herein 'crustaceans'), cephalopods, and fish, and is particularly common among species that undergo daily vertical migration (DVM; see Table 1) (Denton, Gilpin-Brown & Wright, 1972; Herring, 1976; Claes *et al.*, 2014).

Bioluminescence can also be used for conspecific communication, as has been documented in lightning bugs (Hexapoda: Lampyridae), flashlight fish (Anomalopidae), and ostracod (seed shrimp) crustaceans (Herring, 2000, 2007; Buck & Case, 2002; Hellinger *et al.*, 2017; Jägers *et al.*, 2021). In the ocean, sexually dimorphic bioluminescent displays have been reported in fishes (McFall-Ngai & Dunlap, 1984; Ikejima *et al.*, 2008; Chakrabarty *et al.*, 2011; Davis *et al.*, 2014), cephalopods (Voight, 1995), and crustaceans (Oakley, 2005; Morin & Cohen, 2010), which may suggest a role in mate recognition (Herring, 2000, 2007). In some fish, orbital or caudal photophores may be enlarged in one sex, indicating a potential role in sexual signalling and courtship (Herring, 2000; Kenaley, 2009; Davis *et al.*, 2020). Pelagic colonial tunicates called pyrosomes, lanternfishes, and crustaceans including copepods, ostracods, and euphausiids are known to respond to a luminous stimulus with their own illuminations (Herring, 2000).

(3) Bioluminescent decapods

Within crustaceans, bioluminescence is known in ostracods, copepods, decapod shrimps, euphausiids (krill), amphipods, and lophogastrids (Herring & Locket, 1978; Herring, 1981, 1985; Bowlby, Widder & Case, 1991; Oakley, 2005). Luminous secretions are the most common form of bioluminescence within crustaceans and are produced by many pelagic ostracods, calanoid copepods, shrimps, and lophogastrids (Herring, 1985). Photophores are highly variable among ostracods, copepods, amphipods, and shrimps and may be internal or external, and lensed or unlensed (Herring, 1985). This taxonomic review is restricted to bioluminescence in decapod crustaceans, for which it has only been confirmed in shrimps (suborders Dendrobranchiata and Pleocyemata, infraorder Caridea). See Fig. 3 for a diagram of the generalised anatomy of a decapod shrimp. A round pigmented spot at the base of the fixed finger on the chelipeds of the crab, *Hypsophyrs* (now *Lamoha*) spp. (Pleocyemata: Brachyura) has previously been suggested to be a photophore (Williams, 1974), although there is currently no supporting evidence, and a light-emitting function cannot be assumed without further observation of live specimens (Williams, 1976).

Although bioluminescence in decapod shrimps has been reviewed previously (Herring, 1976, 1985), herein we integrate recent studies with historic taxonomic literature concerning bioluminescence and provide a synopsis of light organ type using updated taxonomy. The functional roles of bioluminescence remain unknown for many taxa, and this review compiles the available information from experimental and quantitative studies and provides suggestions for how marine decapods

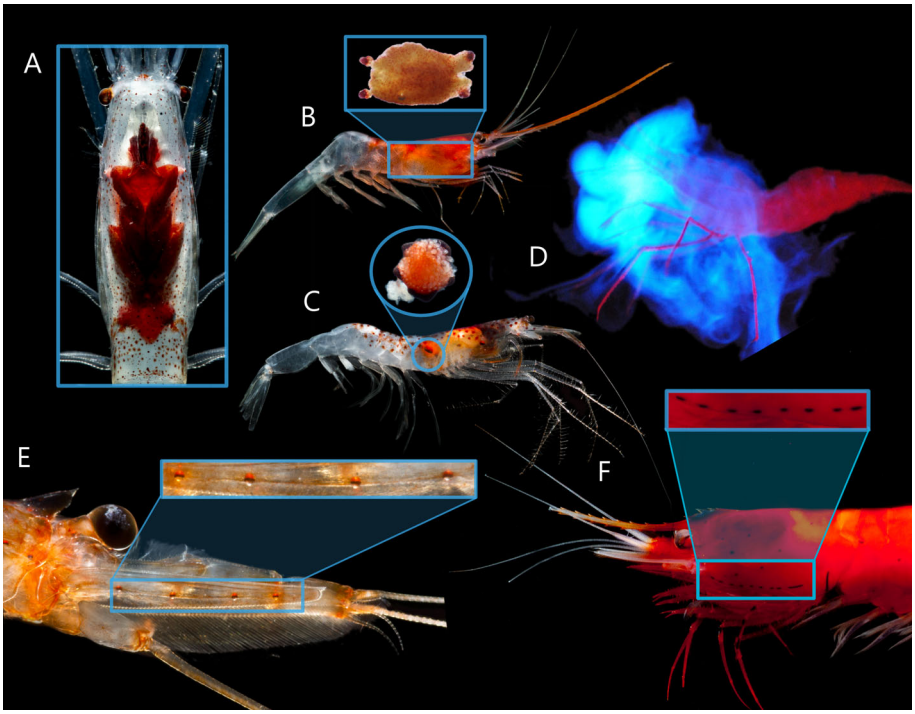

Fig. 1. Modes of bioluminescence in decapods and light organ types. (A) dorsal view of the organs of Pesta of *Parasergestes armatus*. (B) *Plesionika richardi*, enlarged area showing a dorsal view of dissected internal photophores. (C) *Deosergestes henseni*, enlarged portion showing a dorsal view of the posterior lobes of the organs of Pesta. (D) Luminous secretions of *Heterocarpus ensifer*. (E) *Challengerosergia talismani*, enlarged portion showing lensed photophores of the antennal scale. (F) *Systellaspis debilis*, enlarged portion showing pigmented lensed photophores of the lateral carapace. Photograph credits: D. Fenolio (A, B, C, E, F), T. Frank (B inset) and S. Johnsen (D).

may use light in camouflage, communication, and defence. We examine all pelagic, benthopelagic, and deep benthic shrimp families to provide the most comprehensive analysis of bioluminescence in decapod shrimps to date. Additionally, we compile an exhaustive taxonomic list of known bioluminescent species including detailed information on light organ type and bioluminescent mode.

II. TAXONOMIC REVIEW OF BIOLUMINESCENCE IN DEEP-SEA SHRIMPS

(1) Dendrobranchiata

(*a*) *Sergestoidea: Acetidae*

Recent morphological revision of Sergestoidea recovered several new families including Acetidae, a monogeneric family comprising 15 species [14 *Acetes* spp. + *Acetes* (formerly *Peisos*) *petrunkevitchi*] that is not currently accepted by the World Register of Marine Species (WoRMS). This recent taxonomy was recognised by Simões *et al.* (2023). Acetidae is distinguished from Sergestidae by the presence of an elongated third antennal segment, and only five segments or fewer on the fourth and fifth pereopods (Vereshchaka, 2017). *Acetes* spp. are commonly found in coastal and estuarine habitats ranging from marine to freshwater in tropical and temperate regions of the world and are a major target for commercial fisheries in the Indo-West Pacific. Although recent morphological studies state that *Acetes* spp. lack light organs entirely (Vereshchaka, Lunina & Olesen, 2016*a*; Vereshchaka, 2017), historic literature suggests otherwise. Okada (1928) remarked upon the presence of two pairs of red organs on the uropod of *Acetes japonicus*, which he suspected may have been statocysts or organs of similar function. To investigate further, longitudinal sections of the uropods were examined and 'the anterior spot, which is larger than the posterior, has no corresponding organ in any other Crustacea' (Okada, 1928, p. 310). Additionally, Okada (1928, p. 310) stated 'Prof. H. Coutière who has examined my sections, suggests that the organs may be photogenic', but due to the lack of evidence was hesitant to assign a luminescent function. Omori (1975, p. 20–21) stated that 'it is most probable that *Acetes* produce steady emission of greenish-blue light', and that fishermen frequently remarked upon a luminescent glow in the sea associated with nighttime swarms of *Acetes* shrimps. In our review of the literature, nearly all *Acetes* species were reported to have red spots on the uropod, which we speculate are dermal photophores based on the anatomical position and histology of the spots, the ecology of the animals, and previous reports by fishermen (Omori, 1975; see online Supporting

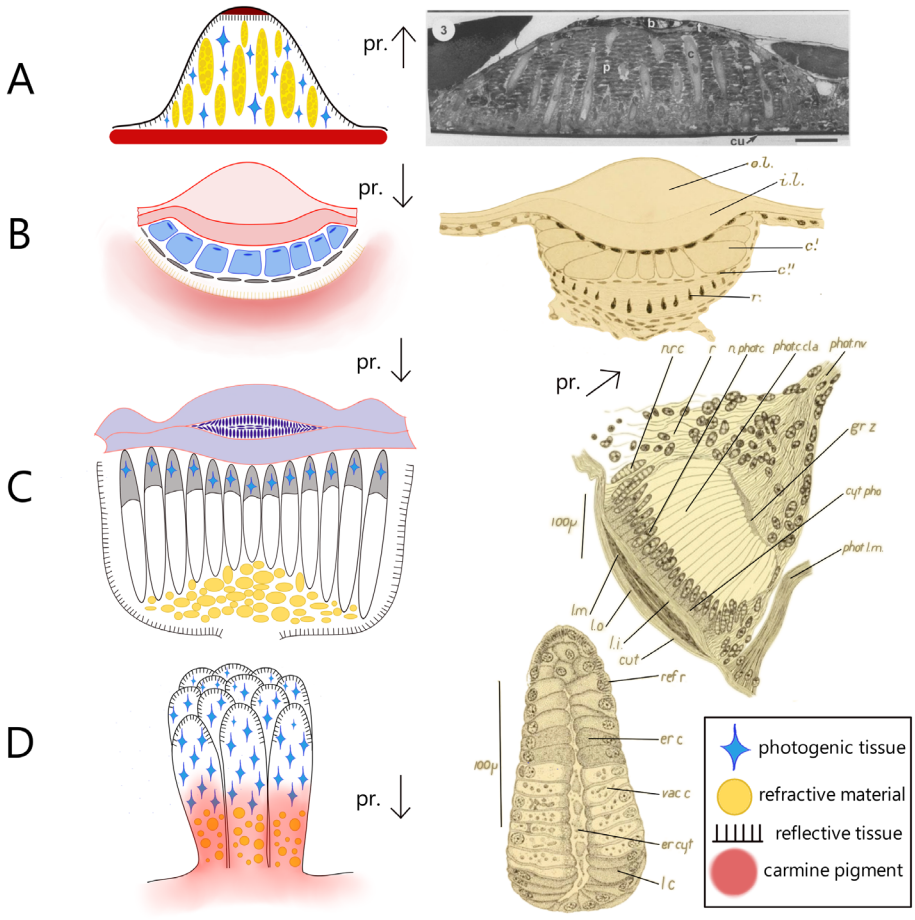

Fig. 2. Diversity of photophore structure in decapod shrimps. (A) Diagram of an unlensed photophore of a sergestid shrimp (left) and histology from Nowel *et al.* (2002) (right). *b*, blood vessel; *c*, columnar cells; *cu*, cuticle; *p*, darkly staining material in photogenic cells; *t*, thin tapetal layer. (B) Diagram of lensed photophore of a sergestid shrimp (left) and schematic from Kemp (1910*a*) (right). *c*′, first cellular layer; *c*″, second cellular layer; *i.l.*, inner layer of lens; *o.l.*, outer layer of lens; *r.*, reflector or striated layer. (C) Diagram of pigmented lensed photophore of oplophorid pleopod (purple shading indicates pigmented lens derived from cuticle; grey shading in columnar cells indicates portion of cell with photogenic material) (left) and histological schematic from Dennell (1940) (right). *cut*, cuticle; *cyt pho*, cytoplasm of photogenic cell; *gr z*, granular zone; *l.i*, inner layer of lens; *lm*, middle layer of lens; *l.o*, outer layer of lens; *phot c cla*, clear area of photogenic cell; *phot.l.m.*, longitudinal muscle of photophore; *phot. nv*, photophore nerve; *n phot c*, nucleus of photogenic cell; *nrc*, nucleus of reflector layer; *r*, reflector. (D) Diagram of a cross section through a lobe of the organs of Pesta of Sergestidae (left) and a histological schematic of one of several tubules comprising each lobe of the organs of Pesta from Dennell (1940) (right). *er c*, erupting cell of tubule; *er cyt*, erupted cytoplasm lying within lumen of tubule; *l c*, 'lens' cell; *ref r*, refractile rods; *vac c*, vacuolated cell. The adjacent to each image depicts the direction of proximity towards the body (pr). In all cases, emitted light is in the opposite direction to the arrow.

Information, Table S1). A recent range expansion record of *Acetes sibogae sibogae* in Japan reported a red spot on the ventral side of the carapace between the last pair of pereopods and two red spots on the uropod, and provided photographic evidence of these (Fukuchi, Hanamura & Imai, 2017). No record of red spots could be found for *Acetes marinus*, although it morphologically resembles a freshwater species with suspected photophores, *A. paraguayensis* (Omori, 1975). No support for potential bioluminescence could be obtained for *A. binghami*, *A. johni*, and *A. natalensis* but the literature is limited for these species. Some species within Acetidae have several designated subspecies, and it is unclear if there is any variation in the distribution of red spots among subspecies. We speculate that these red spots are dermal photophores and that at least some species within *Acetes* are bioluminescent.

(*b*) *Sergestoidea: Luciferidae*

Shrimps within the family Luciferidae are quite distinct in morphology, with elongate eyestalks, a laterally compressed body, absence of branchiae (location indicated by parentheses above pereopods in Fig. 3), and lack of fourth and fifth pereopods in all species (Vereshchaka, 2017). This family is represented by only two epipelagic genera: *Lucifer* spp. are oceanic and exhibit sexually dimorphic eye morphology, while *Belzebub* spp. are neritic with no documented sexual

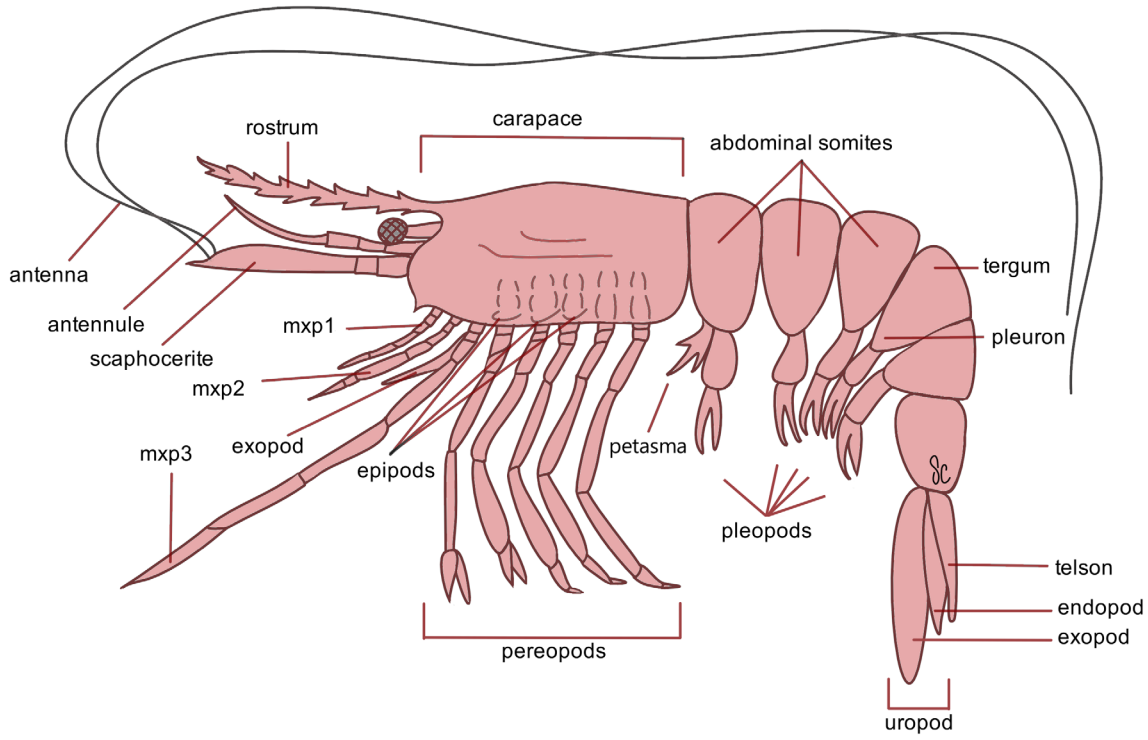

Fig. 3. Anatomy of a decapod shrimp. mxp, maxilliped.

dimorphism (Vereshchaka, Olesen & Lunina, 2016*b*). Although recent literature regarding this family states that dermal and hepatic photophores are absent in Luciferidae (Vereshchaka *et al.*, 2016*b*; Vereshchaka, 2017), Burkenroad (1937) remarked upon the 'scarlet spherule' of the telson of *Lucifer typus* and *Belzebub* (formerly *Lucifer*) *faxoni* and states it 'to be not a simple pigment spot but a ball of cells invested within a tunic of chromatophores' (Burkenroad, 1937, p. 328). Several published photographs show small, dark reddish, spots at the base of each pleopod and along the pereopods (Naomi *et al.*, 2006; Saraiva, Pinheiro & Santana, 2018; Khalaf, Naser & Yasser, 2019). These red spots can be located in photographs for every species within the family, except for *B. intermedius* (see Table S1). We suspect these spots may be light organs, however, it remains uncertain if photophores are truly present in any species within Luciferidae.

(*c*) *Sergestoidea: Sergestidae*

Sergestids are among the most abundant shrimps in the ocean and play an important role in the pelagic ecosystem as they contribute to the carbon pump, transporting carbon through DVMs (Vereshchaka, 2009; Vereshchaka, Lunina & Sutton, 2019). Sergestid shrimps are important prey items for larger, commercially harvested species, and some species with large, shallow aggregations comprise fisheries of their own (e.g. *Eusergestes similis*, *Lucensosergia lucens*, *Sergestes arcticus*) (Omori & Hamner, 1982; Bishop, Omori & Muranaka, 1989; Vereshchaka, 2009). They harbour an impressive array of bioluminescent organ types and patterns (Fig. 4) (Golightly *et al.*, 2022) and species within this family occupy the epi-, meso-, and bathypelagic zones of all oceans across the globe (Vereshchaka, 2000, 2009; Vereshchaka, Olesen & Lunina, 2014). Until recently, Sergestidae contained only two genera: *Sergia* and *Sergestes*. Sergestidae now contains 15 genera based on recent revisions. In this review, we follow use of the suffixes *-sergia* and *-sergestes* to identify the two major morphotypes (Judkins & Kensley, 2008; Vereshchaka *et al.*, 2014). The *-sergestes* species are semi-transparent with red chromatophores scattered anteriorly and are easily characterised by the presence of internal photophores derived from a modified hepatopancreas (Yaldwyn, 1957; Foxton, 1972). In the *-sergestes* group, these light organs are referred to as the organs of Pesta (Fig. 4C). As *-sergestes* shrimps are mostly transparent with an opaque mass in the body cavity, the organs of Pesta camouflage the shrimps *via* counterillumination (Warner *et al.*, 1979). The *-sergia* species are uniformly red to purple in colour and are characterised by the presence of dermal photophores which may or may not include a cuticular lens (Foxton, 1972; Vereshchaka, 2000) (Fig. 4A, B). Interspecific variation of photophore patterns has proved a reliable diagnostic character in fresh material as *-sergia* species can possess between 0 and over 350 photophores, depending on the species (Vereshchaka, 2000; Nowel *et al.*, 2002). Photophores in Sergestidae are abundantly distributed across the ventral and lateral sides of the body, eyestalks, and appendages (Kemp, 1910*a*; Foxton, 1972; Vereshchaka, 2000). These photophores are connected to blood vessels and are thought

Fig. 4. (A) *Gardinerosergia splendens*, enlarged portion showing unlensed photophores of the uropod. (B) *Challengerosergia hansjacobi*, enlarged portion showing lensed photophores of the lateral carapace. (C) *Allosergestes pectinatus*, enlarged portion showing posterior lobe of organs of Pesta. Photograph credits: D. Fenolio.

to be used primarily for counterillumination (Nowel *et al.*, 2002). It is important to note that several -*sergia* species lack photophores entirely, including *Sergia tenuiremis*. In this species, Welsh & Chace (1938) reported finding organs suspected to be luminous in the coxa of the fifth pereopods, however, re-examination showed that this was a misinterpretation of coagulated material from the vas deferens (Dennell, 1940, 1955).

(i) Organs of Pesta. In -*sergestes* spp., the organs of Pesta are a bioluminescent organ derived from the hepatopancreas and comprise ventrally directed luminous tubules which contain anterior, mesial, and posterior lobes (see Fig. 2D) (Foxton, 1972; Herring, 1981). The proximal region of each tubule is an opaque white colour, and the cells here contain many small lipid spheres, which act as a diffuse reflector for the distal end of each tubule (Herring, 1981). The medial region of each luminous tubule produces an intense blue-green fluorescence, which may be attributed to photoexcitation of the luciferin, coelenterazine (Dennell, 1940; Herring, 1981; Latz, 1995). The cells found in the medial region contain many membrane-bound paracrystalline bodies, which are thought to be responsible for light production and fluorescence, and dense particles, which are known to be refractive platelets to help guide the light ventrally (Herring, 1981; Latz, 1995). The distal tips of each tubule are a deep blue colour in life, likely due to a retroreflective layer like that of the *tapetum lucidum* found in the eye (T. Frank, personal communication) and are dorsally surrounded by small lipid droplets associated with a red carotenoid pigment of the hepatopancreas, which is thought to conceal luminous gut contents (Warner *et al.*, 1979; Herring, 1981). Reflector cells of each organ form a curved surface, determining the direction in which light is emitted. The light is typically directed downwards as the organs of Pesta are statocyst-mediated and are capable of rotation (Herring, 1981; Latz & Case, 1982; Latz, 1995; Nowel *et al.*, 1998).

(ii) Unlensed photophores. Unlensed photophores in sergestids are fairly simple in structure and are typically embedded within the membranous tissue beneath the cuticle (S. B. Collins & H. D. Bracken-Grissom, personal observations) (see Fig. 2A). In unlensed photophores, the cuticle is continuous with that of the body, with no apparent modifications. The organ appears to be composed of fibrous photogenic tissue, interwoven with non-membrane-bound columnar cells. These columnar cells contain a high density of refractive material such as lipids and appear to arise from the periphery of the organ (Nowel *et al.*, 2002). The inner photophore is lined by a reflective layer extending laterally near the cuticle. This reflective layer increases bioluminescent emissions by reflecting misguided light out of the organ, serving functionally as a *tapetum lucidum*. Distally, the photophores are connected to blood vessels

(Dennell, 1940). In fresh material, photophores appear red to purple in colour, with the majority often invisible in preserved specimens, except for those on the antennal scale and the uropod (S. B. Collins & H. D. Bracken-Grissom, personal observations). While there is no lens present in unlensed photophores of sergestids, it is possible that the cuticle may focus light, considering the overall optical properties of this organ and the presence of a *tapetum lucidum* and refractive particles of the columnar cells. However, it is plausible that without a proper lens, the emitted light is diffuse. This would perhaps be beneficial for counterillumination, but further investigation into the optical properties of the cuticle is necessary.

(iii) Lensed photophores. Lensed photophores in sergestids differ from all other lensed photophores discussed in this review by featuring a unique double lens, which forms a small protrusion (bubble) on the exoskeleton (see Fig. 2B). These photophores are extensively distributed along the ventral and lateral sides of the body and appendages, each containing a bubble lens to focus light ventrally (S. B. Collins & H. D. Bracken-Grissom, personal observations). The anatomy of lensed photophores of *Challengerosergia challengeri* were described in detail by Kemp (1910*a*). The external lens of the photophore is formed by modification of the existing two-layer cuticle typical of crustaceans. The outer layer of the lens has a convex shape, while the inner layer of the lens is concavo-convex (see Fig. 2B). The lens is abutted by a layer of eight to ten wedge-shaped cells which are a deep blue colour and are likely photogenic (Kemp, 1910*a*). The wedge-shaped cells are surrounded by a thin layer of a few flattened nuclei, of which the function is unknown. The distal end of the photophore is surrounded by a reflective layer, and the entire organ appears to be encompassed by carmine pigment (S. B. Collins & H. D. Bracken-Grissom, personal observations).

Although the exact function of the bubble lens remains uncertain, the strong correlation between sergestid species possessing lensed photophores and their association with seamounts, slopes, and shelves prompts speculation. Notably, our observation of high shrimp abundance in large swarms near these seafloor features, supported by acoustic data, provides further support for this association. It is suspected that the bubble lens may serve to focus emitted bioluminescence ventrally, while simultaneously preventing lateral dispersion of light (Nowel *et al.*, 2002; Golightly *et al.*, 2022). This mechanism may assist benthopelagic individuals in maintaining concealment from both below and within the water column. This serves to reduce the risk of attracting predators drawn by lateral illumination associated with bioluminescence against the dark benthos (i.e. slope or mount). We have personally witnessed massive swarms of sergestid species with lensed photophores and this has also been documented in the literature (Omori & Hamner, 1982; Bishop *et al.*, 1989). It is interesting to consider a potential role of lensed photophores as flashlights, creating expansive luminous areas within the water column. While this luminous swarming strategy may initially attract visual predators, we speculate these bubble photophores could act to confuse predators and disrupt the perception of individual shrimps within the swarm, as light is emitted by several individuals functioning as a collective defence mechanism. This adaptation may play a role in evading predation, adding to the complexity of bioluminescence in the marine ecosystem. Moreover, morphological examination and analyses of Sergestidae suggests they originated in the benthopelagic environment, and later colonised the water column (Vereshchaka *et al.*, 2014). A recent molecular phylogeny found that lensed photophores have a single origin within Sergestidae (Golightly *et al.*, 2022), and it is possible that lensed photophores may have evolved as a result of extended occupancy of the benthopelagic zone (see Table 1).

(iv) Variation in photophore patterning across sex and distribution range. Sexually dimorphic photophore patterns have been reported in species with lensed and unlensed photophores including *Lucensosergia crosnieri*, *L. lucens*, *Challengerosergia challengeri*, *C. fulgens*, *C. stellata*, *C. talismani*, *Gardinerosergia splendens*, and *Robustosergia robusta* (Herring, 1976, 2007; Omori *et al.*, 1997; Vereshchaka, 2000). In many of the species listed above, the difference in number of photophores between males and females is quite small, and the significance of this difference remains unknown. For example, the photophore counts of *L. lucens* were originally reported as 182 in females and 184 in males (which have an extra pair located between the base of the fifth pereopods; preserved specimens examined from Suruga Bay, 1994) (Omori *et al.*, 1997; Herring, 2007). As this only represents a tiny proportional difference between males and females, it is unlikely that it can be resolved by the visual system of the shrimps. Vereshchaka (2000) reports photophore counts in *L. lucens* of only up to 157 in males, and up to 162 in females [preserved specimens examined from Dr Mortensen's Pacific expedition (1914–15, Suruga Bay), and the *Dana I* (1920–22), *Dana II* (1928–30), and *Galathea* (1950–52) expeditions]. This variation in photophore counts could be due to the difficulty of observing photophores in preserved material or could be the result of examining specimens from different regions. Interestingly, the photophore arrangements of *Phorcosergia grandis* from different geographical areas of the world are known to vary (Crosnier & Forest, 1973; S. B. Collins & H. D. Bracken-Grissom, personal observations), and recent molecular phylogenies have revealed population structure across oceanic basins (Golightly *et al.*, 2022). Speculatively, variations in photophore pattern could represent different species across geographical regions, as photophore pattern has recently been found to act as a driver of speciation in other mesopelagic organisms, such as lanternfishes and dragonfishes (Davis *et al.*, 2014). While the influence of variation in photophore pattern in sergestids is not yet understood, it is important to limit examined specimens to those only from a single region when assessing the presence of sexually dimorphic photophore patterns, as intraspecific variation may occur across different geographical areas.

(v) Vision and conspecific signalling. The lobes of the organs of Pesta in sergestids vary interspecifically in number, shape, and pattern (anterior, mesial, and posterior lobe position)

and can be used as a diagnostic character for species identification in fresh material (Foxton, 1972; Herring, 1981; Schweikert *et al.*, 2020). Due to the morphological variation among *-sergestes* species, it was suggested previously that the organs of Pesta may be used for conspecific recognition (Foxton, 1972). A recent study investigated the visual capacity of three sergestid species by testing for sexually dimorphic eye-to-body size ratios, modelling the visual range at which a bioluminescent signal may be detected, and assessing the maximum possible spatial resolution for each species (Schweikert *et al.*, 2020). This study found that *-sergestes* shrimps appear capable of detecting bioluminescent signals from <1 to ∼6 m in distance; however, the spatial resolution was not sufficient to resolve species-specific patterns in any of the species tested and therefore, the organs of Pesta are likely not used for conspecific recognition (Schweikert *et al.*, 2020). A follow-up study investigating eye size as an ecological predictor of bioluminescence in sergestids updated the distance at which point-source bioluminescence can be detected to 1.11–3.77 m; an ecologically relevant distance over which conspecific recognition may be necessary for processes such as aggregations and copulation (Schweikert *et al.*, 2022). Additionally, this study found a general trend in which sergestid eye size increases with depth, and a correlation between eye size and light organ type, where *-sergestes* species had fast-growing eyes, but reached an overall small eye diameter, and *-sergia* species had a large eye diameter and large eye-to-body size ratios. These findings suggest an increased visual investment in *-sergia* species, and may be a result of smaller, dimmer bioluminescent emissions in dermal photophores than from organs of Pesta (Schweikert *et al.*, 2022). Sexually dimorphic photophore patterns, relatively short detection distance, and increased eye size in *-sergia* shrimps all provide support for the potential role of bioluminescence in conspecific signalling (Schweikert *et al.*, 2022) and future studies should continue to investigate this topic.

(vi) Counterillumination and experimental induction of bioluminescence. Underwater video observations show that sergestid shrimps maintain a horizontal to inclined position in the water column, but never more than 90° towards the surface (Ohta & Omori, 1974; Omori & Ohta, 1981). This observation supported earlier speculation that the organs of Pesta function in counterillumination, although the control of bioluminescence in sergestids remained unknown at the time. An experimental study investigating the functional role of bioluminescence in *Eusergestes similis* successfully demonstrated counterillumination with live specimens (Warner *et al.*, 1979). This study found that sergestid shrimps can produce continuous luminescence for upwards of 130 min given a stimulus, can adjust the intensity of their luminescent output to match that of downwelling light, and can respond to rapid changes in light intensity (Warner *et al.*, 1979). Ablation of the eyestalks terminated bioluminescence in the shrimp, suggesting that illumination of the eyestalks and surrounding tissues is necessary for light production (Warner *et al.*, 1979). Experiments with *Eusergestes similis* showed that both the organs of Pesta and the eyestalks counter-rotate to maintain downward illumination when the animal is displaced from a horizontal position (Latz & Case, 1982). A subsequent study investigated the bioluminescent induction of *E. similis* using chemical and photic stimulation (Latz & Case, 1992). To assess chemical induction of bioluminescence, various treatment groups, comprising live unaltered animals, animals with ablated eyestalks, and isolated organs, were subjected to several different neurotransmitters. Among these, only serotonin (5-HT) proved effective, eliciting maximum luminous emission intensity within 27 min of exposure, and with a latency period of about 6 min in live animals (Latz & Case, 1992). Photic stimuli produced different outcomes based on preconditioning of the animals: previously counterilluminating animals had a latency period of only 2 s, reached half-maximum intensity within 13 s, and obtained a steady-state emission within 25 s (Latz & Case, 1992). Animals that had previously been dark-adapted had a latency period of several minutes and reached half-maximum intensity after 12 min, and a steady-state emission after 25 min (Latz & Case, 1992). These pioneering studies confirmed a role of the organs of Pesta in counterillumination and identified collaboration between these organs and the eyes, although the exact mechanism is still unknown.

The regulation of bioluminescence in sergestids remains controversial as there is currently no record of innervation of the organs of Pesta; however, a neural pathway has long been hypothesised based on the effective stimulation of bioluminescence by serotonin treatment (Herring, 1981; Latz & Case, 1992; Latz, 1995; Frank *et al.*, 2023). Interestingly, the slow induction of bioluminescence in dark-adapted shrimps occurs over a similar timescale to that of chromatophore pigment dispersal within crustaceans, which is known to be under hormonal control, although the rapid response to a photic stimulation of a previously counterilluminating shrimp provides support for a neural pathway (Latz & Case, 1992; Latz, 1995). A recent attempt to map the neuronal tract in sergestids between the eye and the organs of Pesta was unsuccessful, although a combination of RNA sequencing data, shipboard experiments and electrophysiology suggest a possible role of photosensitivity in the organs of Pesta, and that regulation of bioluminescent emissions may occur through a combination of photosensitivity within the organ and light stimuli received by the eye (Frank *et al.*, 2023). Additionally, as the presence of a *tapetum lucidum* is known to functionally extend the sensitivity of photoreceptors in the eyes of invertebrates such as spiders (Land & Nilsson, 2012), it is possible that this reflective layer is playing the same role, increasing the sensitivity of the photoreceptors found in the organs of Pesta. Taken together, the evidence suggests that the organs of Pesta in Sergestidae function in counterillumination, although the regulatory mechanisms remain unknown.

(d) *Sergestoidea: Sicyonellidae*

Sicyonellidae is a recently recovered monogeneric family (Vereshchaka, 2017) comprising four species. *Sicyonella* spp.

are benthopelagic shrimps of the coastal epipelagic and are distinct from Sergestidae in their complete chelae of the first pereopod and reduced fourth and fifth pereopods (Vereshchaka *et al.*, 2016*a*; Vereshchaka, 2017). Although the literature states an absence of internal light organs or dermal photophores, photographs of live specimens of a recently described species, *Sicyonella liui* Chan 2020, reveal a series of red dots distributed throughout the carapace, abdomen, and along the appendages. Additionally, the author describes the colour of this species as 'body pinkish translucent and entirely covered with red dots' (Chan, 2020, p. 1387). It remains unclear if these red dots are chromatophores or photophores, and it is possible that both may be present. The distribution of these dots appears to be like the photophore patterns seen in *-sergia* shrimps, however, it remains unclear whether these dots in *Sicyonella* are light organs.

(*e*) *Penaeoidea: Aristeidae*

Species within the family Aristeidae are medium- to large-sized benthic and benthopelagic shrimps found in the meso- and bathypelagic zones and are targets of deep-sea fisheries along the Brazilian coast, throughout the Mediterranean Sea, and in the Indo-Pacific Ocean (D'Onghia *et al.*, 1998; Kapiris & Thessalou-Legaki, 2001; Pezzuto, Perez & Wahrlich, 2006; de Almeida Alves-Júnior *et al.*, 2019). This family comprises nine genera, of which at least three [*Aristeus*, *Aristaeomorpha*, and *Cerataspis* (formerly *Plesiopenaeus*)] contain bioluminescent species (Fig. 5). At least six species of *Aristeus* have dermal photophores on the appendages (Fig. 5B, C), and photophore patterns are used as a diagnostic character to identify species (Dall, 2001; Chan, Kumar & Yang, 2017). Regarding *Aristaeomorpha*, Dall (2001, p. 411) reported 'a pair of large ventral photophores on the thoracic and abdominal somites with a pattern of smaller photophores on the ventral surface, the scaphocerites, external uropods and most of the other appendages' as a character for the genus, although only confirmed the presence of photophores in a single species, *A. foliacea*. Recent collection of *A. foliacea* in the Florida Straits revealed several series of small, evenly spaced photophores along the rostrum, uropods (Fig. 5D), and many of the appendages (S. B. Collins & H. D. Bracken-Grissom, personal observations). Additionally, large indistinct red spots are located on the base of each abdominal somite near the insertion of the pleopod, reminiscent of those found in *Gennadas* (see Section II.1.*f*). It is unclear if these spots are photophore clusters or dense, expanded chromatophores, and therefore, experimental and histological studies are needed. The photophores of both *Aristeus* and *Aristaeomorpha* are red in colour and appear to be without a pigmented lens. Given that other species of the genera with similar depth range and ecology are bioluminescent, it is likely that two species omitted from

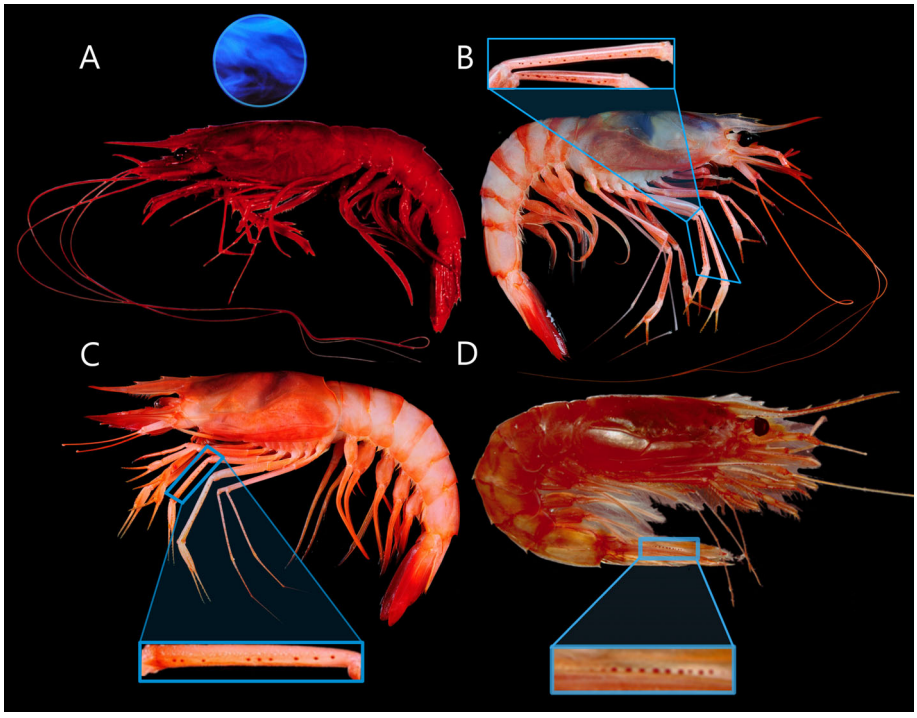

Fig. 5. (A) *Cerataspis monstrosus*, produces luminous secretions as indicated by the blue circle. Photograph credit: W. Pequegnat, 1971, reproduced from Bracken-Grissom *et al.*, 2012). (B) *Aristeus semidentatus*, enlarged portion showing dermal photophores of the second and third pereopods. Photograph credit: T. Y. Chan. (C) *Aristeus virilis*, enlarged portion showing dermal photophores of the second pereopod. Photograph credit: T. Y. Chan. (D) *Aristaeomorpha foliacea*, enlarged portion showing dermal photophores of the uropod. Photograph credit: S. Collins.

Table S1, *Aristaeomorpha woodmasoni* and *Aristeus varidens*, also have photophores, but no reports could be sourced for either species. The genus *Cerataspis* has generated recent molecular interest, resulting in taxonomic changes following the identification of the 'monster larva' *Cerataspis monstrosus* as a larval stage of *Plesiopenaeus armatus* (Bracken-Grissom *et al.*, 2012). Reports of luminous spew have been documented several times for *C. monstrosus* and *C. coruscans*; this is the only known use of luminous secretions within Dendrobranchiata (Herring, 1976, 1985; Gore, 1985; Chan *et al.*, 2008). It remains unknown if other genera of Aristeidae are bioluminescent.

(*f*) *Penaeoidea: Benthesicymidae*

The family Benthesicymidae is comprised of 12 extant genera of deep-sea shrimps: two that are mesopelagic (*Gennadas* and *Notogennema*), four that are bathypelagic (*Altelatipes*, *Amalopenaeus*, *Bentheogennema*, and *Boreogennema*), and six that are restricted to the benthos (*Bathicaris*, *Benthoecetes*, *Benthonectes*, *Benthesicymus*, *Dalicaris*, and *Maorrancaris*) (Vereshchaka, Kulagin & Lunina, 2021*b*). Of the 12 extant genera, only *Amalopenaeus* and *Gennadas* have previously been suspected of having bioluminescent structures. Kemp (1910*a*, p. 640) briefly remarked on the possibility of luminescence in both genera stating they 'may also possess photophores' but did not discuss further. Herring (1985) reported a bluish pigment of the cuticle along the abdomen, near the base of the pleopods and along the pereopods and compared these to the lensed photophores of *Systellaspis* (see Section II.2.*b*). More recently, the arrangement of 'purplish spots' was documented for at least two species (*Gennadas propinquus* and *G. incertus*), although it remains unclear if these are truly light organs (Dall, 2001). Histological examination of *G. valens* discovered lens-shaped modification of the epithelium over the pigmented spots of both the abdomen and pereopods, though this 'lens' was found to be very different from the bubble-like lens in sergestids and the pigmented lens in oplophorids and therefore speculated not to be luminous (Nowel *et al.*, 2002). However, it is noteworthy that lenses of photophores seen in sergestids and oplophorids also arose as a modification of the cuticle, and considering the placement and pigmentation of the spots, the possibility of a lens associated with bioluminescent organs should not be dismissed. Fresh material collected in the Gulf of Mexico provided a chance to observe *Gennadas* spp. (S. B. Collins & H. D. Bracken-Grissom, unpublished observations), and we speculate that the purplish spots on the appendages may be lensed photophores while the purplish spots along the abdomen are perhaps more reminiscent of chromatophores, although further investigation is still needed to discern possible functions of the spots. Additionally, experimental induction of bioluminescence with a dilute hydrogen peroxide solution was unsuccessful in both live and recently dead *Gennadas* specimens. The distribution of potential light organs in *Gennadas* spp. should be documented, and the investigation of bioluminescence in other genera within this family should also be explored.

(*g*) *Penaeoidea: Penaeidae*

Penaeidae is quite a large family with several species playing a role within the aquaculture and fishery industries. With 27 currently accepted genera, the taxonomy of Penaeidae has long been contested, particularly concerning species within the six-genus classification scheme of *Penaeus senso lato* proposed by Farfante & Kensley (1997) (Ma, Chan & Chu, 2011; Yang *et al.*, 2023). Although most species within this family are found near or on the benthos, a few genera represent species that can be found in the meso- and bathypelagic zones of tropical and subtropical oceans. *Funchalia* is a midwater prawn that is strictly pelagic. It is among the most common penaeids collected in midwater trawls, although it is not suspected and has never been reported to be bioluminescent (Fujino, 1973; Wasmer, 1989; Lindley *et al.*, 2001; Lindsay, Hunt & Hayashi, 2001). Examination of fresh material of *Funchalia villosa* collected in the Gulf of Mexico revealed no evidence of bioluminescence. The only other pelagic penaeid is the monospecific *Pelagopenaeus balboae*, for which few scientific reports have been published, none of which mention light organs (Landeira & González, 2018).

Within three deep-sea genera, *Metapenaeopsis*, *Penaeopsis*, and *Parapenaeus*, bioluminescence has not been reported (Watson & Keating, 1989; Mura, Murenu & Cau, 2003; Ohtomi & Nagata, 2004; Sobrino *et al.*, 2005; Paramo & Saint-Paul, 2012; Yang *et al.*, 2015), but more work is needed in deep-sea species. Some penaeid species, such as *Penaeopsis serrata*, undergo daily vertical migrations which overlap with the ecological distribution of other penaeoid shrimps that are known to be bioluminescent, such as *Aristaeomorpha foliacea* (Aristeidae) (Paramo & Saint-Paul, 2012). However, it remains unknown if *P. serrata* or other species within the genus are bioluminescent. Photographs of live *Parapenaeus longirostris* reveal red dots, like those of unlensed photophores. Fresh material of both *P. serrata* and *P. longirostris* should be examined for the presence of potential dermal photophores as it is unclear if these red spots are dense chromatophore aggregations or light organs, and experimental studies should aim to induce bioluminescence in these species.

(*h*) *Penaeoidea: Solenoceridae*

Solenocerid shrimps are deep-benthic and benthopelagic species that contribute to commercial fisheries. The family Solenoceridae includes 10 genera, of which at least four have been reported to produce bioluminescence (Fig. 6). *Hymenopenaeus debilis* is a benthopelagic species with a series of conical photophores located on the ventral side of the body which contain an epithelial lens about the same thickness as the general cuticle, although the photophores are considered to be lensed (Ramadan, 1938; Herring, 1976, 1985; Cartes, Abelló & Torres, 2000; Nowel *et al.*, 2002). Additionally, two other benthopelagic solenocerids, *Hadropenaeus affinis* and *Mesopenaeus tropicalis*, have documented photophore patterns similar to that of *H. debilis*, and are reported to 'consist of a yellow conical portion and a red lens'

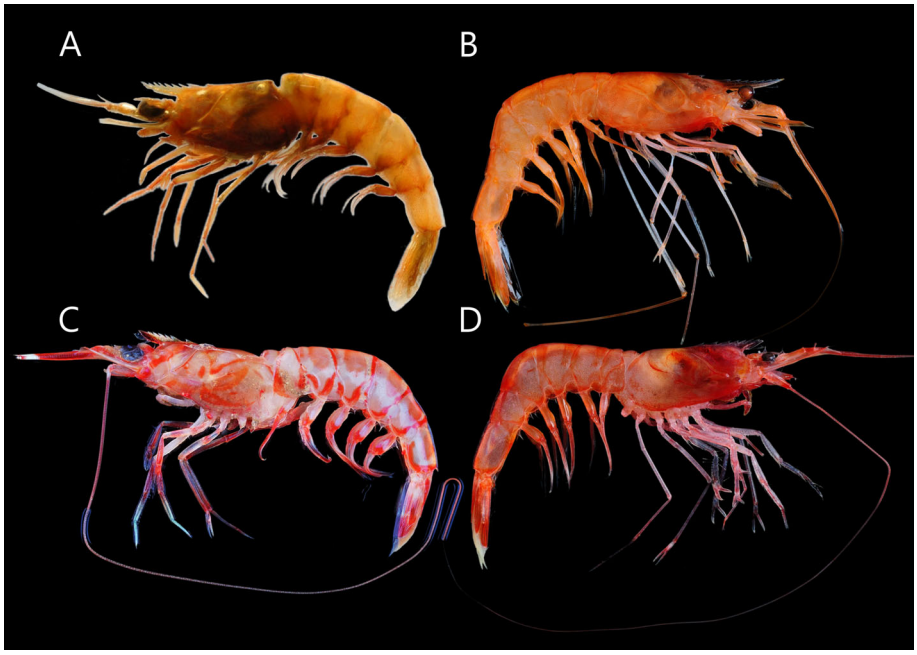

Fig. 6. (A) *Mesopenaeus tropicalis* (photograph credit: Brandi Noble, NOAA). (B) *Hymenopenaeus equalis* (photograph credit: T. Y. Chan). (C) *Solenocera annectens* (photograph credit: T. Y. Chan). (D) *Hadropenaeus lucasii* (photograph credit: T. Y. Chan). All genera represented in this figure are reported to have photophores along the ventral body, although they are not visible in the photographs.

(Farfante, 1977, p. 337). It remains unclear if these photophores are lensed in the same way as other lensed photophores (Sergestidae, Oplophoridae), or if lensed photophores in each group have a unique evolutionary history and morphology. It is interesting that lensed photophores are seen in benthopelagic species within Sergestidae and Solenoceridae, and this may provide support for the evolution of lensed photophores in association with the benthopelagic lifestyle (see Section II.1.*c*; supported by Golightly *et al.*, 2022). The presence of dermal photophores in *Solenocera* has been reported in the literature (Herring, 1985; Dr A. J. Bruce, personal communication cited in Herring, 1985), but no further evidence could be found to support the presence of photophores in any species other than *S. pectinulata* (Crosnier, 1978). It also remains unclear if species within *Hadropenaeus*, *Hymenopenaeus*, *Mesopenaeus* or other genera within the family are bioluminescent.

(2) Pleocyemata: Caridea

(*a*) *Oplophoroidea: Acanthephyridae*

Acanthephyrid shrimps are uniformly scarlet to purple in colour and are found in the meso- and bathypelagic zones of all the world oceans. In 2011, Acanthephyridae was resurrected as a separate family based on molecular and morphological data and can be distinguished from the closely related Oplophoridae by a lack of dermal photophores (see Tables 2 and S2) (Bracken, De Grave & Felder, 2009; Chan *et al.*, 2010; De Grave & Fransen, 2011; Wong *et al.*, 2015; Lunina, Kulagin & Vereshchaka, 2019, 2021). This family comprises eight genera: *Acanthephyra*, *Ephyrina*, *Heterogenys*, *Hymenodora*, *Kemphyra*, *Meningodora*, *Notostomus* and the recently described *Sclerodora* (Vereshchaka, Kulagin & Lunina, 2021*a*). Although *Sclerodora* is not currently accepted as a new genus by WoRMS, due to the unavailability of the name, we recognise the combination of morphological and molecular support for a new genus. Many species are known to participate in DVM, occupying the deeper mesopelagic to bathypelagic zones of the water column during the day, and approaching shallower or surface waters at night. Observations of luminous secretions have been reported for *Acanthephyra* (Nicol, 1958; Clarke, 1963; Herring, 1976; H. D. Bracken-Grissom, personal observations), *Ephyrina* (Herring, 1976), *Meningodora* (Herring, 1976), *Notostomus* (Herring, 1976), and *Hymenodora* (Herring, 1976), and this luminous spew (see Fig. 7) is likely a hepatic product that has been regurgitated from the mouth, presumably used for defence (Herring, 1976, 1985; Chan *et al.*, 2008; Widder, 2010). Although it is suspected and likely that all species within Acanthephyridae are bioluminescent (Herring, 1976, 1985), confirmed reports could only be found for some species (see Table S1 for species list). We report bioluminescence in all species that have either been directly observed producing luminous secretions or from which the experimental induction of bioluminescence upon maceration of hepatopancreas tissue was successful. This method is consistently successful in species that have also been observed producing luminous secretions while alive.

(*b*) *Oplophoroidea: Oplophoridae*

The family Oplophoridae comprises three genera, *Janicella*, *Oplophorus*, and *Systellaspis*, which all are most abundant

Table 2. An abbreviated taxonomic list of bioluminescent decapod shrimps. New reports are indicated in bold. Asterisks indicate that we report bioluminescence with speculation; while there is mounting evidence of the presence of light organs in these groups, further research is required to confirm this. 'Photophores' refer to unlensed dermal light organs, except where lensed photophores are specified. See Table S1 for full list of bioluminescent species reported in this review.

Suborder: infraorder	Superfamily	Family	Modes of bioluminescence reported in this review
Dendrobranchiata	Penaeoidea	Aristeidae	Photophores, secretion
		Benthesicymidae*	**Lensed photophores ***
		Penaeidae*	**Photophores ***
		Solenoceridae	Lensed photophores
	Sergestoidea	**Acetidae***	**Photophores ***
		Luciferidae*	**Photophores ***
		Sergestidae	Photophores, lensed photophores, organs of Pesta
		Sicyonellidae*	**Photophores ***
Pleocyemata: Caridea	Oplophoroidea	Acanthephyridae	Secretion
		Oplophoridae	Lensed photophores, secretion
	Pandaloidea	Pandalidae	Internal photophores, secretion, photophores*
	Pasiphaeoidea	**Pasiphaeidae**	Secretion, **photophores**

in the mesopelagic zone (Cardoso & Young, 2005). Like Acanthephyridae, oplophorid shrimps emit bioluminescent secretions from the mouth (S. B. Collins & H. D. Bracken-Grissom, personal observations for all three genera) but uniquely also have dermal photophores (Fig. 8) (Herring, 1976, 1985). All three genera within this family have photophores along the ventral surface of the body, as well as on the eyes and appendages (Nowel *et al.*, 1998). Unlike sergestids, photophores within an individual are not uniform and the morphology of photophores is highly

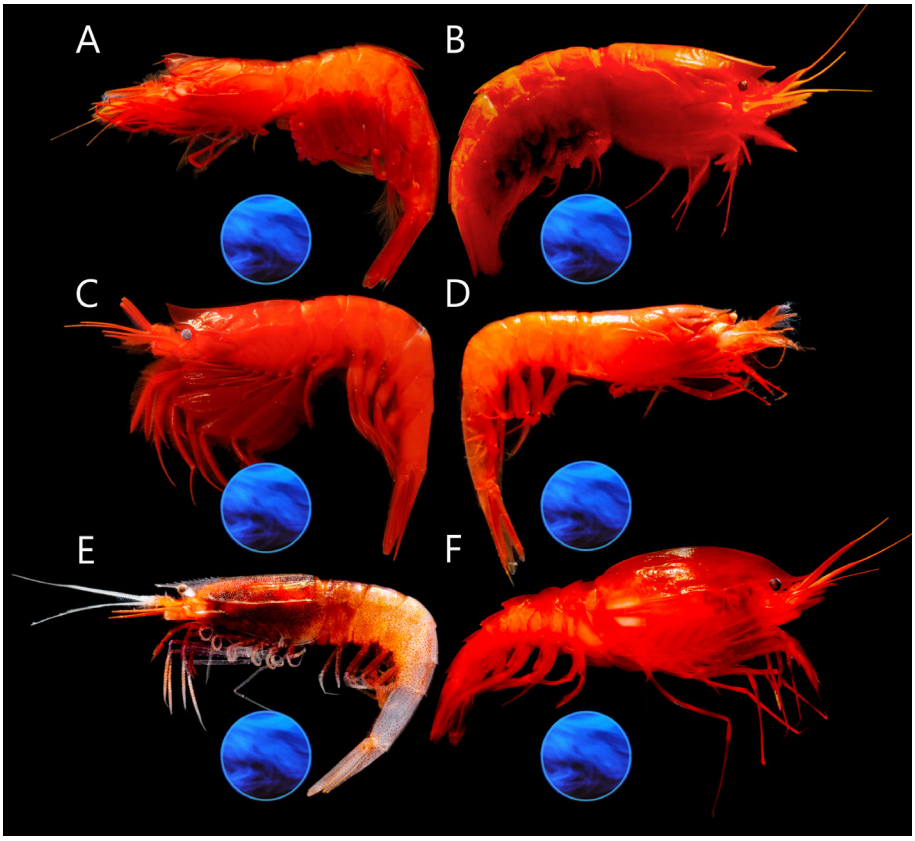

Fig. 7. (A) *Acanthephyra stylorostratis*. (B) *Acanthephyra* sp. (C) *Ephyrina benedicti*. (D) *Hymenodora gracilis*. (E) *Meningodora vesca*. (F) *Notostomus gibbosus*. All species produce bioluminescent secretions, as indicated by the blue circles. Photograph credits: D. Fenolio.

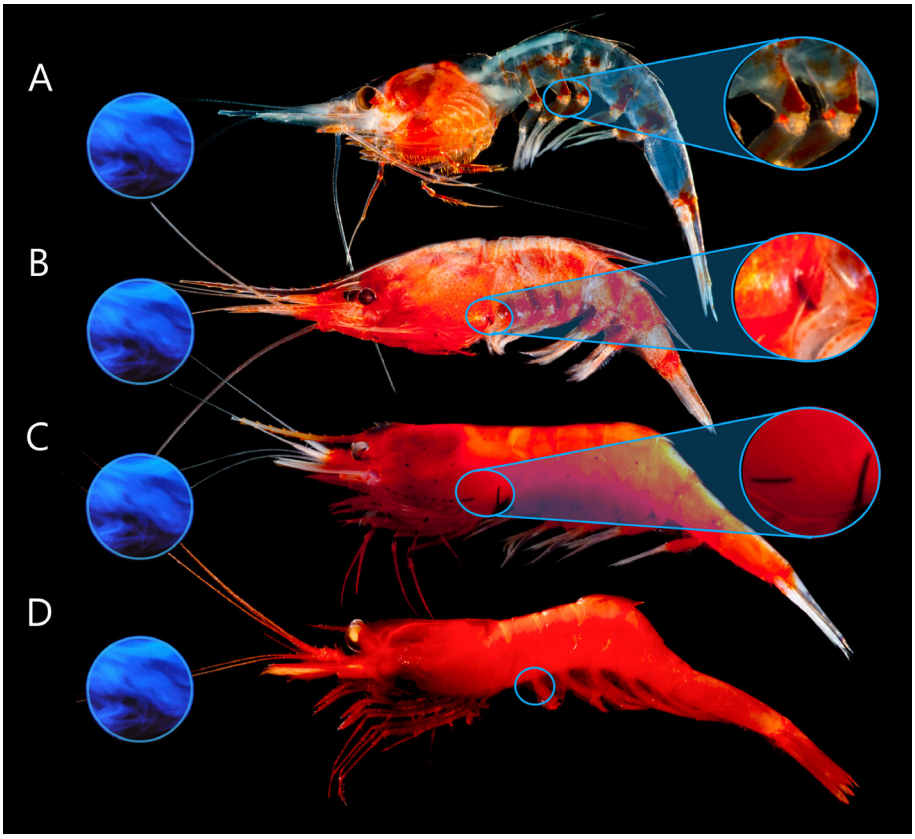

Fig. 8. (A) *Janicella spinicauda*. (B) *Oplophorus gracilirostris*. (C) *Systellaspis debilis*. (D) *Systellaspis cristata*. Enlarged portions show lensed photophores of the pleopods, transverse streak, and transverse and lateral streaks of the carapace, respectively. A blue circle over the junction of the pleopod and abdomen indicates the location of photophores not visible in *S. cristata*. All species produce bioluminescent secretions, as indicated by the blue circles. Photograph credits: D. Fenolio.

variable across the body. Kemp (1910*a*) and Dennell (1940) both discuss the anatomy and structure of photophores of several oplophorid species, within which, four major structural types can be discerned (discussed briefly in Sections II.2.*b.i–iv*): those of the pleopods, those of the fifth thoracic limb, the transverse streak of the carapace, and the well-developed organs of the carapace. Kemp (1910*a*) and Dennell (1940) both remarked upon the clear connection of the photophore to nervous fibres in several photophore types, although recent studies with more updated imaging technology found no evidence of direct innervation (Nowel *et al.*, 1998). Although photophore complexity is highly variable, all photophores seem to be composed of the same cell types (see Fig. 2) (Nowel *et al.*, 1998). Experimentally, treatment with serotonin has been effective in producing a luminous response in the photophores of Oplophoridae (Herring, 1985). However, a coelenterazine solution in sea water was unsuccessful in inducing photophore bioluminescence in live specimens of *Systellaspis debilis* despite multiple attempts (S. B. Collins & H. D. Bracken-Grissom, personal observations). To date, Oplophoridae has been the only family within the infraorder Caridea in which dermal photophores have been described. However, we report here, for the first time, dermal photophores in Pasiphaeidae (see Section II.2.*d*) and speculatively in Pandalidae (see Section II.2.*d*), expanding our current knowledge of bioluminescence in pelagic decapods.

(i) Pleopod photophores. The pleopod photophores of oplophorids are located on the distal coxa of all five pleopods (Dennell, 1940; Nowel *et al.*, 1998). The lens is double convex in shape and is composed of three layers (Fig. 2C). The inner and outer layers are derived from typical layers of the cuticle, whereas the middle layer exhibits greater density and non-uniformity (Kemp, 1910*a*; Dennell, 1940). Variability in shape and density of the nuclei act to form multiple layers within the middle layer, resulting in a total of five layers of differing density across the lens. Dennell (1940, pp. 329–330) remarks upon these layers 'forming a distinct optical combination' and states 'such an elaboration of structure must have a marked effect on its functional properties'. Proximal to the lens is an array of radial photogenic cells. These cells lack cytoplasm in their proximal regions, forming a functionally clear space two-thirds the length of the cell (Dennell, 1940). The distal end of the photogenic cells is convex in shape and they are abutted by conical cells of granular material, with the apices directed towards the entrant nerve

bundle. A pair of photophores on the uropod appear to be of the same structure (Kemp, 1910*a*; Dennell, 1940).

(ii) Photophores of the fifth thoracic limb (third maxilliped). Photophores are present as a luminous patch on the proximal carpus and as a long patch on the distal propodus of the fifth thoracic limb of several oplophorid species. The structure of these photophores is similar to those of the pleopods, although with a few interesting differences. The most notable difference is that the photophores of the fifth thoracic limb (third maxilliped) lack an obvious lens (Dennell, 1940). The other major difference is that the photogenic cells of these organs are in graduated degrees of development, forming regions of different cellular development. The photogenic cells are lined with a reflective cell layer, and these photophores are separated from the integument by a highly vacuolated zone (Dennell, 1940).

(iii) Transverse photophore streak. There is an obvious transverse streak of photophores on the wall of the carapace behind the coxa of the fifth pereopod in many oplophorid species, and they are much less developed and simpler in structure than those of the pleopods. The structure of the transverse streak resembles the structure of the photophores of the fifth thoracic limb, although is distinct in a few aspects. There is no apparent lens-like modification of the cuticle over these photophores other than slight thickening and the graduation of the photogenic cells appears to be inverted relative to those of the fifth thoracic limb (Dennell, 1940). Additionally, the photogenic cells converge into a cone as in other photophore types, although these photophores lack refractive material (Dennell, 1940).

(iv) Photophores of the carapace. The photophores of the carapace are well developed and structurally complex. The lens is double convex in shape and semi-lunar when in surface view, creating a bubble similar to those of sergestids, though apparently different. As with the pleopod photophores, the lens is composed of three layers. In these photophores, the middle layer of the lens is not uniformly constructed and variable in thickness, presenting unique optical properties (Dennell, 1940). The photogenic cells are similar in structure to those of pleopod photophores, although entirely devoid of cytoplasm. The distal end of the photogenic cells is semicircular, and lined with a reflective layer (Dennell, 1940).

(v) Tilt and mobility of photophores. Photophores within Oplophoridae are capable of rotation, although it is unclear if this manipulation is regulated by vision or statocyst mediation (Nowel *et al.*, 1998). While there are photophores all along the bodies of oplophorid shrimps, it is not known if those on the carapace and abdomen are capable of tilt rotation. Tilt rotation mechanisms of photophores on thoracic appendages is logical as the maxillipeds are often used in food capture and consumption and the pereopods for food manipulation and swimming, and rotation of the photophores is necessary to maintain ventral illumination for camouflage. However, we speculate that the photophores of the carapace and abdomen are not capable of tilt rotation due to the fact that rotation is less important in stationary regions of the body. Photophores within Oplophoridae are not known to be directly connected to the nervous system, which may suggest an indirect mechanism of control, although more research is required (Nowel *et al.*, 1998).

The photophores of the pleopods are supported by an arrangement of musculature including a primary and secondary longitudinal muscle and a loop muscle (Dennell, 1940). Further evidence of photophore mobility is seen in a modification of the lens. Near the periphery of the photophore, the lens is folded, allowing it to be displaced as the photophore is tilted back and forth with pleopodal movement (see Fig. 2) (Kemp, 1910*a*; Dennell, 1940; Nowel *et al.*, 1998). Photophores along the dactylus of the third maxillipeds are simple in organisation and are attached to a ligament at the apex of each ovoid- to conical-shaped photophore (Nowel *et al.*, 1998). Upon extension and flexion of the joint, the longitudinal photophore muscle rotates the photophores backward, and the photophore loop muscle rotates the photophores forwards along the apices, allowing emitted light to be ventrally directed at all times [see Nowel *et al.* (1998) for full explanation]. Photophores supported in this way by musculature provides evidence for their utilisation in counterillumination, but it remains unclear whether they have additional mobility or other functions.

(vi) Photophores and vertical distribution. Recent morphological analysis of *Systellaspis* spp. revealed four species groups: *S. braueri* group (containing four species), *S. cristata* group (containing two species), *S. debilis group* (containing two species), and *S. lanceocaudata* group (containing three species). Although molecular analysis supports the species groups within *Systellapsis*, the deeper relationships between genera have not yet been resolved (Lunina *et al.*, 2019). In the Gulf of Mexico, all three genera and all four *Systellaspis* species groups are found, and all representative species have photophores except for the deepest living oplophorid, *S. braueri*. An exceptional example of the functional role of photophores within Oplophoridae is that of *S. cristata*, which has very faint red photophores only on the base of the pleopods that can be easily missed if not examined carefully (S. B. Collins & H. D. Bracken-Grissom, personal observations) (see Fig. 8D). To the best of our knowledge, this is the first report of photophores in *S. cristata*, and the structure of these organs has not yet been investigated. As the vertical distribution of *S. cristata* is deeper than that of other oplophorids but shallower than *S. braueri*, this species provides support for the restriction of photophores to shallower species, likely with a function of counterillumination. This suggests that loss of photophores occurs when vertical distributions exceed the depths where counterillumination is beneficial. As photophores could only be confirmed in representatives of the *S. cristata*, *S. debilis*, and *S. lanceocaudata* species groups, it is possible that all species within the *S. braueri* group lack photophores, but examination of fresh material is needed to confirm this.

(vii) Pigmented lens and spectral sensitivity. The lens of photophores in oplophorid shrimps is heavily pigmented, usually either purplish-blue or orangish-red (S. B. Collins & H. D. Bracken-Grissom, personal observations). In live *Oplophorus gracilirostris* specimens collected in the Gulf of Mexico,

juveniles had red-pigmented photophores, and adults had purple-pigmented photophores, suggesting a potential ontogenic change in pigment colour as adults transition to deeper waters. It also remains unknown if the photophores of *S. cristata* are equipped with a red lens or if they are without lenses entirely. The pigmented lenses overlying the photophores in oplophorids have been suggested to act as a spectral filter (Herring, 1985), perhaps narrowing the wavelength of their own bioluminescent emission (in a similar way to how light is received by the human eye when wearing coloured sunglasses). Studies concerning the spectral maxima of visual pigments in the eyes reveal that species within Oplophoridae are unique in bearing a near-ultraviolet photopigment (390–410 nm), in addition to the typical blue-sensitive photopigment (468–540 nm) as seen in other midwater shrimps (Latz, Frank & Case, 1988; Cronin & Frank, 1996; Herring, 1996; Warrant & Locket, 2004; Gaten, Shelton & Nowel, 2004; Wong *et al.*, 2015). The combination of a pigmented lens overlying the photophores and the unique dual-sensitivity detection system raises the possibility that oplophorid shrimps may be using the pigmented filter as a private channel for communication using photophores, particularly those with a purple lens.

(viii) Visual ecology and bioluminescence. The compound eyes of oplophorid shrimps are relatively large in size, perhaps to increase sensitivity to bioluminescence in the deep sea (Welsh & Chace, 1938). Additionally, a histological study of the retinae of oplophoroid shrimps revealed significant variation in rhabdom shape and distribution in association with depth, in which the dorsal region of the retina in photophore-bearing species such as *S. debilis* and *O. gracilirostris* contains rhabdoms typical of shallow-water species, while the rest of the eye contains densely packed multilobed rhabdoms (Gaten, Shelton & Nowel, 2003). The spaced rhabdoms of the dorsal region are surrounded by cytoplasmic fluid to increase the refractive difference, resulting in an area of high resolution to downwelling light, but poor sensitivity due to the presence of fewer rhabdoms. The densely packed rhabdoms of the remainder of the eye have high sensitivity with poorer resolution, but are likely effective in resolving differences in contrast within the water column (Gaten *et al.*, 2003). A recent study investigating vision within Oplophoridae revealed a high diversity of visual opsins and differential gene expression across vertically migrating individuals, suggesting that expression of opsins in the eye may be correlated to spectral tuning during DVM (DeLeo & Bracken-Grissom, 2020). This study also performed RNA sequencing on the photophores and found that the opsins expressed in the photophores are identical to those found in the eyes (DeLeo & Bracken-Grissom, 2020). A second study (Bracken-Grissom *et al.*, 2020) used the same approach combined with *in-situ* hybridization, immunohistochemistry, and shipboard experiments to provide evidence that these light organs not only emit light but can also detect light (= photophore photosensitivity). The unique retinal morphologies and spectral sensitivities of the eyes suggest that oplophorid shrimps may be capable of differentiating bioluminescent emissions from photophores (possibly those with different coloured lenses) from that of luminous secretions, and the recent discovery of photophore photosensitivity suggests that light emission may be regulated and received through a combined effort of the eyes and photophores.

(c) *Pandaloidea: Pandalidae*

Shrimps within the family Pandalidae are distributed throughout the ocean, ranging from shallow coastal waters to the deep benthos and are among the most biodiverse carideans. Pandalids are a cold- or deep-water group and are identified by reduced or absent chelae of the first pereopods and a subdivided carpus of the second pereopod (Chace, 1992). Bioluminescence within Pandalidae is present in several modes, of which luminous secretions and internal photophores have been confirmed (Herring, 1985) (Fig. 9). Luminous secretions have long been reported with certainty for midwater *Heterocarpus* spp. and have been documented in laboratory studies stimulating bioluminescence in *H. ensifer* (Herring, 1976; Johnsen *et al.*, 2012), *H. grimaldii* (Herring, 1976), *H. sibogae* (Herring, 1976; Chan *et al.*, 2008) and *H. oryx* (H. D. Bracken-Grissom, personal observations). It is unknown if other species of *Heterocarpus* are bioluminescent and although it is likely, further investigation is needed. Herring (1976) remarked upon a single report of *Plesionika alcocki* producing a luminous spew but noted that confirmation is still needed for this species. Chan *et al.* (2008) report *Plesionika* as a pandalid genus that produces luminous spews in addition to *Heterocarpus*, but it remains unclear if bioluminescence was observed or speculated in *Plesionika*. A single species currently known as *Plesionika richardi* (syn. *Stylopandalus richardi* and *Parapandalus richardi*) has been reported to have internal hepatic photophores (Dennell, 1940, 1955; Herring, 1976, 1985; Christoffersen, 1990), and our recent unpublished work has confirmed the presence of internal photophores in live *P. richardi* specimens collected in the Gulf of Mexico. Experimental induction of bioluminescence with both a dilute hydrogen peroxide solution and coelenterazine solution in sea water was unsuccessful in both live specimens and dissected organs. However, Dennell (1940, 1955) reported observations of luminescence in the internal organs of live specimens, confirming that the internal organs of *P. richardi* are bioluminescent. Additionally, Herring (1976) reported dermal photophores located on the pleopods of *Parapandalus* (*Plesionika*), although no species name is mentioned. We speculate this report likely concerns *P. richardi* as Kemp (1910*a*) and Dennell (1940, 1955) report the presence of deep red spots which are presumed to be photophores on the first three pairs of pleopods in this species. Although these have not yet been observed by us, we suspect dermal photophores are likely present. Johnsen *et al.* (2012) also mentions bioluminescent secretions in benthic *Parapandalus*, but the species was not documented. It is also unclear if any *Plesionika* species emit luminous secretions or if any other species have internal photophores.

Thalassocaris and *Chlorotocoides* were previously thought to comprise their own family, Thalassocarididae, until a recent phylogenetic study placed these two genera within Pandalidae, dissolving Thalassocarididae (Liao *et al.*, 2019). Both genera

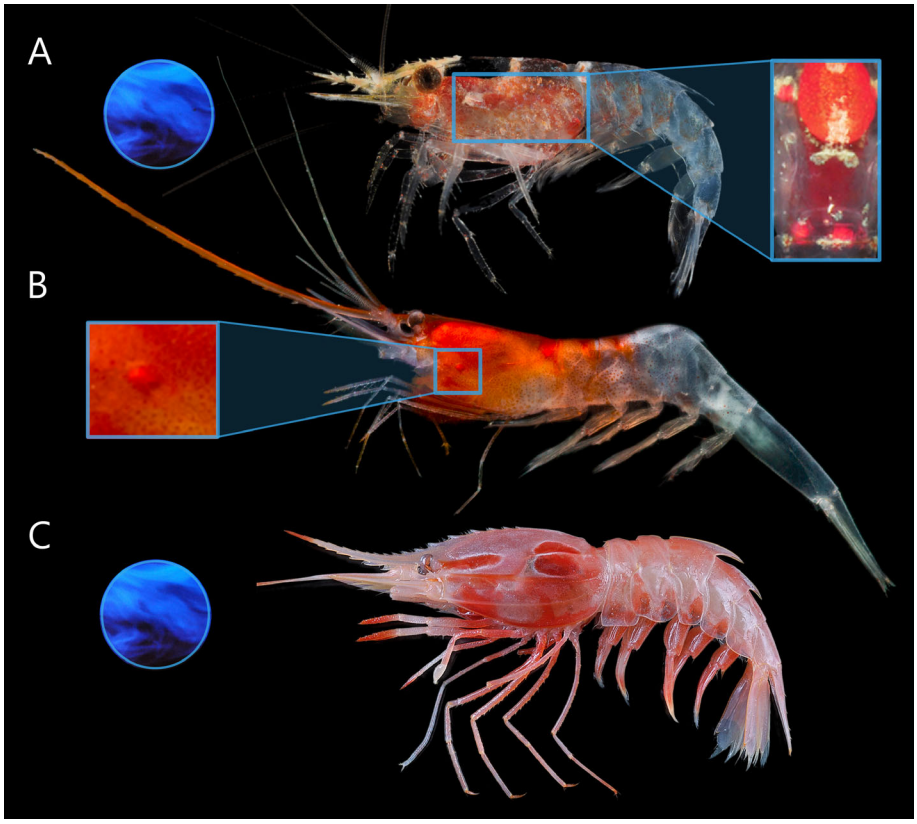

Fig. 9. (A) *Thalassocaris crinata*, which produces luminous secretions as indicated by the blue circle. Enlarged portion showing a dorsal view of the internal photophores. Photograph credit: G. Paulay. (B) *Plesionika richardi*, enlarged portion showing the anterior lobe of the internal photophores. Photograph credit: D. Fenolio. (C) *Heterocarpus ensifer*, which produces luminous secretions as indicated by the blue circle. Photograph credit: S. Johnsen.

have been reported to use bioluminescence, although the mechanism requires further investigation for species within both genera. Herring (1976, 1985) reported luminous secretions in *Thalassocaris*, and hepatic photophores in both *Thalassocaris* and *Chlorocoides*. Christoffersen (1989) reported dermal photophores (one pair at the base of the maxilla, and one pair on the posterior side of the basis of the fifth pereopod) in both *Thalassocaris* and *Chlorotocoides*, but re-examination of these organs revealed that these photophores are in fact internal and similar to those found in *P. richardi* (Menon & Williamson, 1971). Observations of live specimens of *Thalassocaris crinita* found luminous secretions of blue-green bioluminescence in addition to the presence of internal photophores (Herring & Barnes, 1976; Marin & Chan, 2011) making this the first record of bioluminescence in the form of internal photophores plus luminous secretions for a species within Decapoda. It remains unknown if luminous secretions occur in any other *Thalassocaris* species or in any species of *Chlorotocoides*.

It appears that bioluminescence is much more common within Pandalidae than previously reported. We speculate that the secretory emissions of bioluminescence from *Heterocarpus*, *Plesionika (?)*, and *Thalassocaris* are used for defence, as seen within the families Acanthephyridae and Oplophoridae. The hepatic photophores of *Plesionika*, *Thalassocaris* and *Chlorotocoides* likely function for counterillumination, like that seen in the *-sergestes* group, or potentially conspecific signalling. The possible dermal photophores on the pleopods of *Plesionika* also require attention, as their presence first requires documentation before speculating on any function. If future morphological, histological, and experimental evidence supports the presence of photophores in *P. richardii*, it would be the first record of a species to be bioluminescent through a combination of internal and dermal photophores, both within Pandalidae and within Decapoda.

(*d*) *Pasiphaeoidea: Pasiphaeidae*

Pasiphaeidae comprises seven genera distributed worldwide, with most species occupying the meso- and bathypelagic zones (Tavares & Cardoso, 2006). Within Pasiphaeidae, bioluminescence has only been reported with certainty in one species, *Glyphus marsupialis*, which is known to produce luminous secretions (Herring, 1976, 1985; Chan *et al.*, 2008) (Fig. 10C). Herring (1976) reported potential luminescence in the eye of *Pasiphaea tarda*, although this may be a misinterpretation of the reflecting *tapetum lucidum* layer of the retina, which likely plays a role in increasing the sensitivity of photoreceptors in the eye (Schwab *et al.*, 2002). Herring (1985) reported

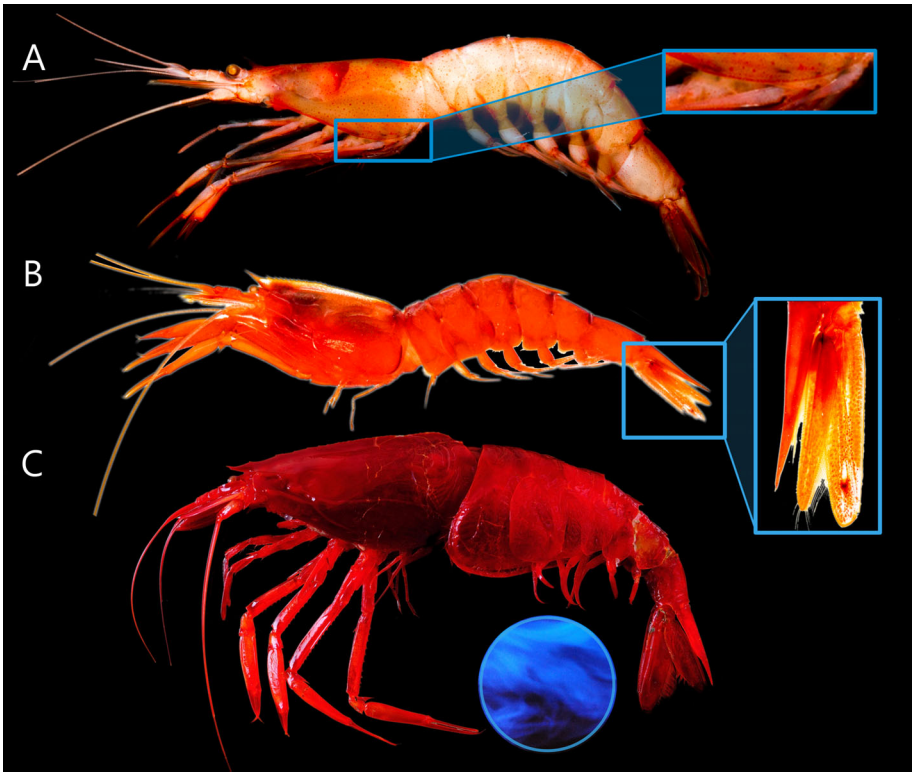

Fig. 10. (A) *Pasiphaea princeps*, enlarged portion showing suspected photophores on the bottom margin of the lateral carapace. Photograph credit: D. Fenolio. (B) *Eupasiphae gilessi*, enlarged portion showing suspected photophore of the uropod. Photograph credit: D. Fenolio. (C) *Glyphus marsupialis*, which produces luminous secretions as indicated by the blue circle. Photograph credit: T. Y. Chan.

luminescence in *Parapasiphae* but did not specify the type or species. More recently, identification of a new species led to morphological revision of the entire genus, and no evidence of photophores was reported (Wasmer, 2005), although this does not eliminate the possibility of luminous secretions in species of *Parapasiphae*. *Parapasiphae kensleyi* has a unique double eye in which the retinae are entirely separated and the corneas each have a different axis of orientation (Wasmer, 2005). This is the first report of a double eye in a deep-sea shrimp, we suspect it could function to detect bioluminescent flashes in the water column, as eyes with variable retinal morphologies in Oplophoroidea have been reported to increase overall sensitivity in the eye likely with this role (Gaten, Shelton & Herring, 1992; Gaten *et al.*, 2003, 2004). Finally, there is a single report of luminescence in *Leptochela*, although the origin of this luminescence remains unclear, and further investigation is needed (Herring, 1985). The secretory luminescence of *Glyphus marsupialis* is likely used for defence, as is suspected for other groups.

Recent observations of a live specimen of *Eupasiphae gilesii* collected in the Gulf of Mexico led to the discovery of dermal photophores in Pasiphaeidae (Fig. 10B, see Tables 2 and S2). A single large, red organ is located on the distal end of the uropodal exopod, in which the borders are clearly defined and surrounded by red pigment. We interpret this to be a light organ based on both morphology and location, although emission of bioluminescence could not be observed as the animal was dead upon collection. This photophore appears to be without a cuticular lens, although, histological examination is needed to confirm this. Additionally, the posterolateral sides of the carapace and abdominal somites, and the dorsal abdomen are all lined with dark red borders. This was also seen in photographs of another pasiphaeid species in the Gulf of Mexico, *Pasiphaea princeps* (Fig. 10A), and though we have not yet observed live specimens, we suspect these dark borders to be a series of fused photophores. We report here, for the first time, the likely presence of dermal photophores in Pasiphaeidae, and the possibility of bioluminescence in other pasiphaeid species should be investigated further.

III. DISCUSSION

The production of light through bioluminescence is a common phenomenon in the ocean, particularly in the deep sea, with an estimated 94 independent origins across the metazoan Tree of Life (Lau & Oakley, 2021). Many organisms utilising bioluminescence also participate in DVM, implying that bioluminescence may allow these animals to

remain concealed as they transition through different light environments. Within Decapoda, bioluminescence is restricted to dendrobranchiate and caridean shrimps, and can exist in several modes, including luminous secretions, internal hepatic photophores, and dermal photophores with or without an overlying lens. In this review, we report bioluminescence, either with certainty or speculatively, in 157 species spanning 12 families across Decapoda. This increases the number of reported families from five to 12 (see Tables 2 and S2) and increases the number of bioluminescent species by 65% (see Table S1). Within Dendrobranchiata, bioluminescence is reported in Sergestidae, Aristeidae, and Solenoceridae, and speculated to be present in Acetidae, Luciferidae, Sicyonellidae, Benthesicymidae, and Penaeidae (Table 2; Fig. 11). While additional studies are needed to confirm bioluminescence in the families where it is suspected to be present, if our speculations are validated, Sicyoniidae would be the only family within Dendrobranchiata not to have at least one bioluminescent species. It thus appears that bioluminescence is a common trait among dendrobranchiate species, suggesting a single origin within Dendrobranchiata. Within Caridea, bioluminescence is reported in Acanthephyridae, Oplophoridae, Pandalidae, and Pasiphaeidae (Fig. 11). While bioluminescence has been well documented for Oplophoroidea (Acanthephyridae and Oplophoridae), further experimental and histological studies are needed to investigate bioluminescence in Pandalidae and Pasiphaeidae, as uncertainty remains regarding the modes of bioluminescence in some species.

Secretory bioluminescence is known in the family Aristeidae (Dendrobranchiata), and the families Acanthephyridae, Oplophoridae, Pandalidae, and Pasiphaeidae (Caridea). Bioluminescent representatives of these families typically occupy the meso- and bathypelagic zones of the ocean. Release of a bioluminescent secretion in the dark environment of the deep sea is thought to act as a 'smoke screen', startling predators and allowing shrimps to escape (Haddock *et al.*, 2010). Some species with secretory luminescence are benthopelagic, including *Heterocarpus*, *Plesionika*, *Thalassocaris* (Pandalidae), and *Cerataspis* (Aristeidae). While these shrimps interact with both the benthos and water column, secretory luminescence is likely most effective in the water column as the benthic environment presents different visual pressures (mud, silt, hard-bottom structures), although it is probably used as a defence mechanism in both environments (Johnsen *et al.*, 2012). Luminous secretions were previously thought to be the most common form of bioluminescence among decapod shrimps (Herring, 1976, 1985). However, we report herein more species with dermal photophores (74 species; see Tables S1 and S2) compared to both internal photophores (44 species) and luminous secretions (48 species). We acknowledge that documentation of secretory luminescence is difficult, and this should be targeted in future studies alongside how different modes of bioluminescence (secretory and photophores) have evolved across the shrimp tree of life.

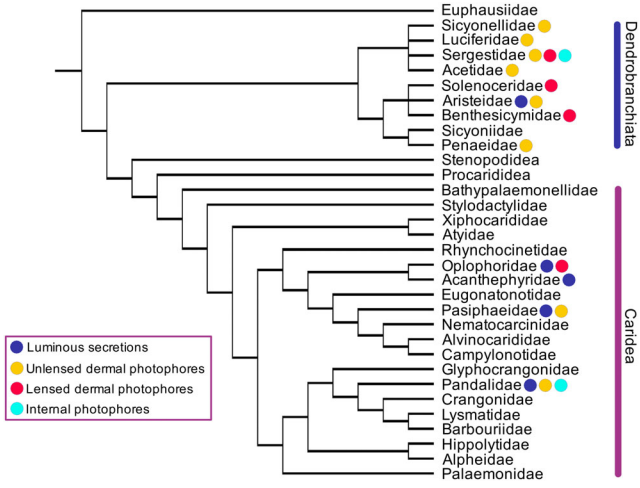

Fig. 11. Cladogram of family relationships among decapod shrimps. This tree is based on a combination of molecular phylogenies from Li *et al.* (2011), Aznar-Cormano *et al.* (2015), and Wolfe *et al.* (2019). Bioluminescent modes for each family known or suspected to be bioluminescent are indicated by coloured circles. All families without symbols are not suspected to be bioluminescent. Not all shrimp families are included due to uncertainty of their phylogenetic position.

Internal, hepatic photophores are found in Sergestidae (Dendrobranchiata), and Pandalidae (Caridea). As with the organs of Pesta of the *-sergestes* group, it is likely that the hepatic organs of *Plesionika richardi*, *Chlorotocoides spinicauda*, and *Thalassocaris* spp. play a role in counterillumination. Dennell (1940) described in detail the anatomy of the hepatic organs of *P. richardi*, and discussed their morphology compared to that of the *-sergestes* group, attributing the differences in structure to their systematic placement (see Fig. 11). Dennell (1940) also considered the significance of the functionality of these organs, and the important role that they may play in the deep-sea environment, attributing to this the apparent convergent evolution of hepatic photophores across Decapoda. Dennell (1940) suggested that the hepatic organs of both *-sergestes* species and *P. richardi* function to illuminate the gills, likely for wide-field illumination to conceal the body. However, later experimental demonstrations of counterillumination in a *-sergestes* species (Warner *et al.*, 1979; Latz & Case, 1982, 1992; Latz, 1995) provided clear evidence that hepatic photophores, at least in Sergestidae, are used for counterillumination to camouflage the visceral mass of the body. Kemp (1910*a*) and Dennell (1940) reported the presence of luminous glandular streaks in the branchial chamber of many *-sergestes* species, and photophores in the same position in *-sergia* species (Kemp, 1910*a*; Dennell, 1940). We have examined previously collected material preserved in glycerol and failed to confirm the presence of light organs within the branchial chamber. We suggest that the previous reports may relate to damaged internal organs of Pesta or dermal photophores on the branchial region of the carapace. Our observations of lensed photophores in *Challengerosergia talismani* were congruent with early observations of *C. challengeri* (Kemp, 1910*a*) having a single photophore near the anterolateral margin of the carapace, positioned entirely beneath the

cuticle and facing towards the posterior end of the animal. Given its position centred beneath the visceral mass, we posit that this photophore, like the organs of Pesta, is likely used to camouflage the visceral mass, and that the angle of the photophore likely directs light onto the gills, illuminating the entire branchial chamber, and thereby, most of the lateral sides of the body. Observation of hepatic photophores in live animals indicate that the luminous tubules comprising these organs appear proximal to the hepatopancreas in *P. richardi* while in *-sergestes* species they are arranged along the distal edge of each luminous lobe. While the organs of Pesta of Sergestidae have been well researched, we suggest employing a combination of histological and experimental approaches on pandalid species with hepatic photophores to explore the function of these organs in more detail.

Dermal photophores are known to be present in Sergestidae, Aristeidae, Solenoceridae, Oplophoridae, and Pasiphaeidae, and speculatively in Acetidae, Luciferidae, Sicyonellidae, Benthesicymidae, Penaeidae and Pandalidae (see Tables 2 and S2). Photophores of Sergestidae may be lensed or unlensed and are abundant on the ventral and lateral sides of the body and appendages. In Aristeidae, photophores are unlensed and distributed along the rostrum, ventral body, uropods and appendages. Photophores in Solenoceridae are restricted to the ventral side of the body and apparently bear an external lens, although these have not yet been observed in live specimens by the authors. In Oplophoridae, photophores are lensed and distributed over the carapace, on the ventral body, and along the appendages including the pleopods, uropods, and eyes. In Pasiphaeidae, the most obvious photophores appear only on the uropods. Dermal photophores in Pandalidae are suspected on the pleopods, and suspected photophores in Acetidae appear to be restricted to the uropods. In Luciferidae and Penaeidae, photophores appear unlensed and are suspected on the pleopods and uropods, and in Sicyonellidae, photophores appear to be unlensed, but are suspected to have a similar distribution to those of Sergestidae. In Benthesicymidae, the possible photophores are thought to be lensed and are distributed on the appendages and on the base of each abdominal pleura. For all groups in which the presence of photophores is still speculative, more research is warranted, including experimental chemical induction of bioluminescence.

Lensed photophores have been reported for Sergestidae, Solenoceridae and Oplophoridae, and are speculated to be present in Benthesciymidae (see Tables 2 and S2). It is important to note that our category 'lensed photophores' refers simply to the presence of an additional external lens, however the morphologies of these photophores can be very different (see Fig. 2). It is likely therefore that each type of lensed photophore has an independent origin, and that the functional role of the lens may be unique for each. In Sergestidae, lensed photophores are only found in benthopelagic species (Fig. 2B). As the external lens forms an incomplete convex bubble over the photophore, it is likely that this lens functions to focus emitted bioluminescence ventrally from all photophores: a strategy to avoid lateral detection from predators against seamounts, shelves, and slopes while also concealing themselves from predators below *via* counterillumination. Lensed photophores in Solenoceridae are known only in benthopelagic species, and do not appear to have the bubble shape seen in Sergestidae, although detailed studies are still required. Further examination is needed to describe the lensed photophores of solenocerid shrimps and to determine the extent of similarity with lensed photophores seen in other families. The lensed photophores of Oplophoridae are unique in containing a pigment (Fig. 2C). This may act as a spectral filter to narrow the emission spectrum, allowing animals to discriminate photophore emissions from those of luminous secretions, possibly for conspecific recognition. The suspected light organs of *Gennadas* (Benthesicymidae) should also be explored with current imaging methods, particularly given that Nowel *et al.* (2002) reported a modified epithelium overlying the purple spots.

Whether bioluminescence exists in other taxonomic groups not examined here remains uncertain. All families that occupy the water column or deep benthos were reviewed (Fig. 11, some families not included due to uncertainty in phylogenetic position), and we found no reports of bioluminescence in Sicyoniidae, Bythocarididae, Bresillidae, Disciadidae, Campylonotidae, Bathypalaemonellidae, Eugonatonotidae, Nematocarcinidae, Chlorotocellidae, Psaliodpodidae, and Stylodactylidae. Some taxa such as *Bythocaris* (Bythocarididae) (Bowman & Manning, 1972; Abele & Martin, 1989) and *Parapasiphae* sp. (Pasiphaeidae) (Wasmer, 2005) have highly sensitive eyes presumed to detect bioluminescence, either for predator avoidance or prey detection. Although they are not known to produce bioluminescence, it is possible since specialised eyes are also found in species that produce luminous secretions, such as Oplophoroidea (Gaten *et al.*, 1992, 2003, 2004).

For all families in which we speculate bioluminescence, future studies are needed to confirm the presence of light organs using current histological techniques. For taxa with few records, such as *Petalidium* (Sergestoidea: Petalidiumidae; Vereshchaka, 2017), the limited information suggests an absence of light organs (Vereshchaka & Lunina, 2015). As nearly all sergestoid shrimps are suspected or known to be bioluminescent, it seems possible that *Petalidium* may also have hepatic or dermal photophores. No live material has ever been studied, with collected specimens often moribund or in poor condition, and the presence of photophores is typically difficult to detect in preserved material. Similarly, *Nematocarcinus* (Nematocarcinidae), has never been reported to be bioluminescent, but reports of 'posteroventral spots' (Komai & Segonzac, 2005, pp. 355, 357–358, 361, figs 9c, 11c and 12e) on the sixth abdominal somite should be confirmed using fresh material to determine whether these spots are simply texture in the exoskeleton or are chromatophore or photophore assemblages.

IV. FUTURE ILLUMINATIONS

Many challenges exist when researching deep-sea organisms, and many organisms collected in midwater and benthic

trawls are moribund upon examination due to changes in temperature and pressure as they are brought to the surface. As bioluminescence plays an integral role in the ecology of many deep-sea crustaceans, the study of live animals is essential to determine the presence of light organs. Luminous secretions were thought to be the most common form of bioluminescence in decapod shrimps, we show herein that instead dermal photophores are most common and are present in every family of bioluminescent decapods except Acanthephyridae (Fig. 11, Tables 2, S1 and S2). We are certain that additional species are likely to produce luminous secretions, and more investigation is warranted, particularly within Pandalidae. Homogenisation of the hepatopancreas in fresh and frozen specimens produces luminescence in species known to secrete bioluminescence, and this seems to be a reliable alternative to *in-situ* observation when investigating bioluminescent secretions in decapod crustaceans (Herring, 1985). However, as many species also consume bioluminescent prey, it is important to consider that this reaction may be a by-product of luminous gut contents. The experimental induction of bioluminescence in species with both dermal and hepatic photophores is feasible through chemical treatments such as serotonin, dilute hydrogen peroxide, KCl, nitric acid, and acetylcholine and this approach has been foundational in uncovering the phenomenon of bioluminescence in shrimps. However, the success of induction is most pronounced in live, active organisms, and is not guaranteed, necessitating many replicates and a repertoire of chemicals for effective results.

As more studies investigate the visual capacities of deep-sea shrimps, it is likely that insights regarding the roles of bioluminescence in each group will be uncovered. A recent study on sergestid shrimps revealed a correlation between eye size and light organ type, which may suggest a role of bioluminescence in conspecific signalling. Species with dermal photophores were found to have the largest absolute eye size when compared to those with other light organ types (Schweikert *et al.*, 2022). This study also found that sergestid shrimps are capable of detecting bioluminescence from a maximum distance of ∼64 body lengths, which is a relevant distance for swarming species, and suggests that individuals may be able to detect conspecific bioluminescence. Future studies could assess the visual spectral sensitivities of oplophorids together with pigmentation of the lens of the photophore and the spectral emission of their bioluminescence. We suggest that the purple pigment of the lens may filter out longer wavelengths, thereby narrowing the spectral emission band. Combined with the known visual abilities of several oplophorid shrimps [near-ultraviolet sensitivity and expression of multiple medium wavelength-sensitive (MWS) opsins (see Bracken-Grissom *et al.*, 2020; DeLeo & Bracken-Grissom, 2021)] this may allow spectral discrimination among bioluminescent emissions, enabling them to act as private communication channels. It is equally plausible that the pigmented lens is an adaptation to the light environment in which the species lives (i.e. to its vertical depth distribution). In some fishes and squid, a yellow lens in the eye helps to break the camouflage of animals using bioluminescence for counterillumination, providing an example of a pigmented lens associated with the detection of bioluminescence (Denton & Warren, 1968; Somiya & Tamura, 1971; Muntz, 1976; Somiya, 1976, 1979, 1982). Documenting the spectral wavelength of emission for each group and each light organ type could provide insights into the potential use of bioluminescence for communication and the potentially unique roles of bioluminescence across the midwater column and deep benthos.

Much variation exists in light organ types in decapod shrimps, and the morphology and evolutionary history of each bioluminescent group should be assessed independently. Current research is underway mapping light organ types across depth and habitat for Dendrobranchiata and Caridea. The potential use of bioluminescence as a private channel of communication, as suggested here for Oplophoridae, would be a groundbreaking discovery. Although much remains to be understood regarding bioluminescence in decapod crustaceans, by compiling all previously published taxonomic and experimental data, this review provides a detailed account of current knowledge of the language of light in deep-sea shrimps.

V. CONCLUSIONS

(1) We report bioluminescence in 157 species of decapod shrimps spanning 12 families — an increase in bioluminescent decapod species of 65% from a previous review which reported 55 species spanning five families (Herring, 1976).
(2) Bioluminescence may exist in one or several modes in decapods including lensed and unlensed dermal photophores, internal photophores, and/or luminous secretions. We provide an extensive taxonomic list of all reported bioluminescent decapod species with light organ type and bioluminescent modes.
(3) The pigmented lenses in dermal photophores paired with the dual spectral sensitivity visual system in oplophorid shrimps may act as a private communication channel, allowing individuals to differentiate bioluminescent emissions of photophores of conspecifics from those of luminous secretions.
(4) We report photophores in the family Pasiphaeidae based on personal observations of light organs in live specimens, making this the first record of dermal light organs in this family, and increasing the number of representative caridean families with dermal photophores.
(5) Previously, luminous secretions were thought to be the most common form of bioluminescence in decapod shrimps. By contrast, we find dermal photophores to be the most common light organ type across decapod species.
(6) Future research directions include experimental studies investigating the visual capacity of deep-sea shrimps, phylogenetic studies investigating the evolution of bioluminescence across decapod taxa, and molecular studies investigating extraocular photosensitivity.

VI. ACKNOWLEDGEMENTS

We dedicate this manuscript to Dr Tamara (Tam-Bam) Frank whose love for shrimp is contagious and has been an incredible role model for women in marine science. Her patience, guidance and mentorship on deep-sea shrimp, vision and bioluminescence made this study possible. We also acknowledge Dr Stanley W. Kemp, F. R. S., Dr Ralph Dennell, Dr Peter J. Herring, whose research was foundational and inspired our love for glowing decapods. Special thanks to the crew of the R/V *Point Sur*, University of Miami, R/V *Walton Smith* and R/V *Weatherbird* for their assistance in collecting specimens. This research was made possible by grants from the National Science Foundation Division of Environmental Biology Grant # 1556059 (awarded to H. D. B.-G), Biological Oceanography # 2154168 (awarded to H. D. B.-G.) and Graduate Research Fellowship Program # 2034832 (awarded to S. B. C. and H. D. B.-G) the National Oceanic and Atmospheric Administration Ocean Exploration Research (NOAA-OER) grant (#NA170AR0110208; awarded to S. Johnsen and Subaward No. 331461 awarded to T. Frank) and DEEPEND|RESTORE project #NA19NOS4510193 (awarded to H. D. B.-G.), the Gulf of Mexico Research Initiative (GOMRI, DEEPEND), and Florida Institute of Oceanography Shiptime Funding. Special thanks to all members of the CRUSTOMICS lab for discussions and reviews of this manuscript, Angela Ceballos for providing assistance in editing the manuscript, and K. Boswell for his ideas concerning bioluminescence in swarming sergestids. Data are publicly available through the Gulf of Mexico Research Initiative Information & Data Cooperative (GRIIDC) at https://data.gulfresearchinitiative.org, https://doi.org/10.7266/N70P0X3T and https://doi.org/10.7266/n7-1xs7-4n30. Finally, we thank the anonymous reviewers for their feedback. This material is based upon work supported by the National Science Foundation under Grant No. HRD-1547798 and Grant No. HRD-2111661. These NSF Grants were awarded to Florida International University as part of the Centers of Research Excellence in Science and Technology (CREST) Program. This is contribution # 1680 from the Division of Coastlines and Oceans in the Institute of Environment at Florida International University.

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. List of all known bioluminescent decapod species with information on light organ type and mode of bioluminescence.
Table S2. Diversity of bioluminescent organ types across shrimp families.

(*Received 27 September 2023; revised 11 April 2024; accepted 22 April 2024*)