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BIOLUMINESCENCE IN THE CRUSTACEA

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"To observations which ourselves we make
We grow more partial for the observers sake" (Pope)

Contents

The characteristics and distribution of bioluminescence have in recent years been reviewed for the Crustacea in general (Harvey, 1952, 1961; Herring, 1978) and for particular crustacean groups, i.e., amphipods (Herring, 1981a), euphausiaceans (Mauchline and Fisher, 1969; Herring and Locket, 1978), and decapods (Herring, 1976). These provide an introduction to the earlier literature and make it unnecessary to provide a fully comprehensive bibliography here, allowing me to focus upon the more recent work. Only a limited number of crustacean groups are known to include luminous species (ostracods, copepods, amphipods, euphausiaceans, mysids, and decapods). Isolated earlier reports from other groups (Harvey, 1952) have not been substantiated.

Bacterial Luminescence

Luminous bacteria provide the source of light in the luminous organs of a number of fishes and squids. This situation does not occur in the Crustacea but there are several reports of sporadic infections by luminous bacteria rendering certain crustaceans temporarily luminous. This condition was first demonstrated clearly in talitrid amphipods (Giard, 1889; Giard and Billet, 1889) and has subsequently been described in other amphipods, both marine (Bousfield and Klawe, 1963) and fresh water (Bowman and Phillips, 1984). Similar infections have been noted in two isopods and the fresh-water shrimp *Paratya* (=*Xiphocaridina*) (Yasaki, 1927; Haneda, 1955); luminous bacteria have also been reported from *Penaeus indicus* (Krishnamurthy, 1980).

Taxonomic Distribution of Luminescence

Ostracoda

The contribution of ostracods to the luminescence of the sea has been recognised since the mid-eighteenth century. Luminescence was originally described from species of *Cypridina* and *Pyrocypris,* but Poulsen's (1962) revision of the Cypridininae synonymized *Pyrocypris* with *Cypridina* and assigned generic status to

Skogsberg's subgenus *Vargula.* The species in this subfamily whose luminescence has been reported in vivo or in extracts are *V.* (*Cypridina*) *hilgendorfi, V. antarctica, V. norvegica, V. harveyi, V. tsujii, V. bullae, Cypridina* (=*Pyrocypris*) *noctiluca, C. serrata, C. americana,* and *C. dentata.* The last species is almost certainly the correct identity of *Pyrocypris chierchiae,* whose luminescent labral glands were the first to be described (Müller, 1890), and of *Pyrocypris* sp. noted by Tett and Kelly (1973).

The luminescence of all these species is emitted into the sea from the labral glands, structures which become functional in the early embryo (Okada and Kato, 1949). There are up to four types of gland cells in *V. hilgendorfi* (Harvey, 1952) opening via one or more of the five labral papillae. The largest cell type contains yellowish granules and is probably the source of the luciferin and one of the other cell types the luciferase, but no microchemical investigations have yet been undertaken. The ready availability of large numbers of animals and the stability of the dried luminescent material has resulted in this being the first marine luciferin to have been chemically identified (Kishi *et al.,* 1966) and the reaction mechanism has subsequently been studied in detail (references in Hastings, 1983a).

Much less is known concerning the biology of these ostracods. They occur in very high densities (up to 30,000 m^{-2}) in coastal and surface offshore waters (Vinogradov and Voronina, 1962). Recent observations in the northern Indian Ocean have shown that *C. dentata* may be the dominant organism in the neuston at night (cf. Tett and Kelly, 1973) and that the swarms are associated with mating activity (Daniel and Jothinayagam, 1977, 1979). Underwater observations on the complex mating behaviour of *V. harveyi* (Morin and Bermingham, 1980) have reported luminescence associated with vertical spiraling movements and a synchrony of luminous pulses between adjacent groups of animals. A light stimulus produces a luminous response in these ostracods (Haneda, 1940; Tsuji *et al.,* 1970) and all these observations emphasise the degree of control that the animals have over their emission, causing it to appear as clouds of light, glowing spots, or short flashes. It is probable that other species of *Cypridina* and *Vargula* are luminous, and perhaps even some of the other 17 genera in the Cypridininae, for several have glandular labral papillae akin to those with luminous organs. Nevertheless, *Gigantocypris* and *Macrocypridina,* at least, are nonluminous (Herring, 1978).

Other luminous ostracods are found in the family Halocypridae, notably in the genus *Conchoecia.* These are pelagic species, extending into the meso- and bathypelagic realms, whose luminescence has been investigated only recently (Rudjakov, 1967; Angel, 1968). Unlike the Cypridininae the luminous glands are situated only on the carapace margin. They may be present under the rostral incisure, on carapace projections, and/or on the posterior edge of the carapace (Angel, 1968). Luminescence is visible either as a secretion (from the rostral incisure glands) or as point sources within other glands, particularly those on the carapace extensions. Probably all species of *Conchoecia* are luminous. Rudjakov (1967) found differences in the responses of animals taken during the day and the night, with more daytime animals responding to electrical stimulation. No obvious differences were detected in the flash characteristics of different species, sexes, or ages.

Copepoda

Giesbrecht (1895) carried out the first detailed study of copepod luminescence, in the Gulf of Naples. He found that only five of the great many species he investigated were luminous, in the genera *Pleuromamma, Lucicutia, Hetero-*

rhabdus, and *Oncaea.* Since then many other species have been reported to be luminous, but the literature is conflicting and confusing, with the difficulties of accurate observation of these tiny animals being exacerbated by the problems of their identification and of the question of seasonal variations in their responses.

Among the harpacticoids, luminescence has been reported in *Macrosetella gracilis* (Artiomkin *et al.,* 1966; Rudjakov and Voronina, 1967) without additional information. I have observed luminescence in numerous specimens of the related, and superficially similar, species *Aegisthus mucronatus* from sites on the cephalic and caudal regions as well as on some of the limbs. Giesbrecht's (1895) detailed observations on *Oncaea conifera* provide the basis for cyclopoid luminescence. I have been able to confirm many of his conclusions on this species, which has numerous fluorescent photocytes spread over the whole dorsal surface of the body, but not the limbs. Both sexes are luminous, though the male is much smaller. There is a regular segmental pattern of photocytes and the animals produce individual high intensity flashes (cf. Lapota and Losee, 1984) of ~100 ms duration and some longer poststimulus glows (cf. Filimonov and Chumakova, 1969). There is a 1:1 stimulus response at frequencies of up to 10 Hz and eserine induces flashing. As Giesbrecht concluded, *O. conifera* is the *only* luminous species. There have been several reports of luminescence in *Oithona* spp., without additional detail (Rudjakov and Voronina, 1967; Filimonov and Chumakova, 1969; Krylov, 1969) though Giesbrecht could not demonstrate it in his specimens. There are similarly conflicting reports for species of *Corycaeus* (Rudjakov and Voronina, 1967; Lapota and Losee, 1984).

Close observations of luminescing species of *Oncaea* and *Aegisthus* give no indication that there is any secretion to the exterior. Indeed it is clear in *Oncaea* particularly that luminescence appears only within the photocytes and adjacent internal channels. In marked contrast all the luminous calanoid copepods produce external luminescent material from glands opening via pores on the body and/or limbs. A great many calanoid genera have been described as luminous but since many of the reports are unsubstantiated or denied by other workers, the position of many of these genera remains contentious. Clarke *et al.* (1962) reviewed the previous literature and concluded that there was certain luminescence only in the Metridiidae, Heterorhabdidae, Augaptilidae, and Aetideidae. As the authors intimated, the Aetideidae should probably be excluded, as it is based solely on Kiernik's (1908) report of *Chiridius.* Since then there have been reports in *Euchaeta* and *Undinula* (Artiomkin *et al.,* 1966; Filimonov and Chumakova, 1969), *Scolecithrix* (Greze *et al.,* 1966, cited by Filimonov and Chumakova, 1969), *Neocalanus* and *Nannocalanus* (Tett and Kelly, 1973), *Paracalanus, Acrocalanus,* and *Centropages* (Krylov, 1969; Lapota and Losee, 1984), and *Megacalanus* (Herring, 1978). On the basis of the present information it is reasonable to assume that all species of the Metridiidae, Augaptilidae, Lucicutiidae, and Heterorhabdidae are luminous; there are experimental data for all four families. Identification of the site of luminescence in *Megacalanus* (glands on swimming leg 2) adds this genus to the cases of certain luminescence.

The Metridiidae (*Metridia, Pleuromamma,* and *Gaussia*) have been the most extensively studied in recent years (David and Conover, 1961; Clarke *et al.,* 1962; Artiomkin *et al.,* 1966; Rudjakov and Voronina, 1967; Filimonov and Chumakova, 1969; Barnes and Case, 1972; Shevijrnogov, 1972; Evstigneev, 1983; Herring, unpublished), building on Giesbrecht's (1895) earlier work. These copepods have luminous glands variously distributed on the head, body, caudal furcae, and some limbs. They are fluorescent and histological work shows two gland types at each locus, opening through a common pore (Clarke *et al.,* 1962). Several luminous

discharges from each site can be elicited by successive stimuli. The most detailed experimental investigation (Barnes and Case, 1972) showed that *Gaussia* had a minimum response latency of 15 ms and that the discharge decayed as several discrete points of light over a period of up to 80 s. There is no indication of sexual dimorphism in the glandular sites.

A functionally very similar luminescence occurs in the Lucicutiidae and Augaptilidae. In the former the luminous glands are present on the body and limbs, in the latter only on the exopods of swimming legs 3, 4, and 5 (not 2, as suggested by Clarke *et al.*, 1962). The glands are fluorescent in both these families, while in the Heterorhabdidae most, but not all, are nonfluorescent and they occur on the body, limbs, and caudal furcae.

The function of these glands is presumably that of a deterrent or distraction to a predator. Experiments by David and Conover (1961) indicated that the glands were employed when individual *Metridia* were captured by euphausiids. A light stimulus produces a "cascade" response in *Gaussia* which appears to be a similar startle reaction, resulting from physical contact with the walls of the vessel (Barnes and Case, 1972). Luminescence develops early, for nauplii and copepodites of several genera respond to stimulation though the luminescent potential increases with maturity (Giesbrecht, 1895; Rudjakov and Voronina, 1967; Evstigneev, 1983).

Amphipoda

Amphipod luminescence is quite unlike that of the copepods or ostracods in that there is almost always no external secretory product and in some cases accessory tissues are associated with the photocytes. Luminous tissue occurs in both hyperiids and gammarids. Woltereck's (1905) description of "Reflektororganen" in *Scypholanceola* probably referred to modified eyes and the first description of luminous organs is probably that of Fage (1934) in the hyperiid *Streetsia porcella* which has three organs, each contained in a brownish pigment cup, on the coxal and basal articles of pereiopods 6 and 7. He did not observe light emission but similar structures on the sixth and seventh pereionites in *Parapronoe crustulum* luminesce strongly (Bowman, 1967; Herring, 1981a). The organs are directed ventrally and the photogenic core has a greenish fluorescence. The most widespread luminous hyperiids are species of the family Scinidae (Herring, 1967, 1981a). Probably all species are luminous, with characteristic large photocytes generally present on the uropods, antennae, and fifth pereiopods. In *S. marginata* and *S. submarginata* additional photocytes are present over most of the body and other pereiopods. The photocytes are large vacuolar cells associated with an intracellular duct (Lane and Herring, unpublished) and have an intense fluorescence after stimulation. The animals produce flashes of 80–300 ms duration and show facilitation at low stimulus frequencies. Summation occurs at stimulus frequencies >5–10 Hz and eserine induces scintillation. Free-swimming animals flash when touched and the larger species simultaneously adopt a characteristic defensive posture (Herring, 1981a). *Proscina* may also be luminescent. The only other luminous hyperiid is the lanceolid *Megalanceola terranovae* which has photocytes at the distal region of several pereiopods and uropods. Unlike all other amphipods this species produces an external luminous secretion.

Among the Gammaridea there are several luminous lysianassids (Bowman, 1967; Herring, 1981a). Species of *Cyphocaris* have luminous sites in the extended frons, urosome, and uropods. The responses to electrical stimuli are usually complex pulses in response to trains of stimuli, with single flash durations of 1–2 s.

The photocytes are not fluorescent nor are they responsive to adrenergic or cholinergic agents.

A quite different luminous appearance is given by species of *Thoriella* and the *Chevreuxiella/Danaella* complex. *Thoriella* responds from the antenna and uropods, while specimens of the latter generic complex (Thurston, personal communication) luminesce *either* from the expanded maxilliped plate *or* (in inflated specimens) from innumerable point sources over the whole surface of the body. Pulses of 2–4 s duration are produced by any form of irritant stimulus and photocytes have been tentatively identified in histological material.

In all cases amphipod luminescence appears to be a defensive response and its general distribution at the distal extremities may serve to enhance the apparent size of the animal in such circumstances.

Mysidacea

Early reports (Harvey, 1952) suggested luminescence in several genera, but one of the clearest accounts, in specimens of *Gastrosaccus* found on a sandy beach, suggests a bacterial infection. The only incontrovertibly luminous mysids are the giant deep-water species of *Gnathophausia* which produce an intense greenish cloud of light when they are disturbed. The luminescence is produced by a gland in the second maxilla (Illig, 1905) and expelled through a pore on a protuberance of this appendage. It can be repeatedly elicited from captive animals and is presumed to be a defensive tactic. Investigations of other deep-sea genera (e.g., *Eucopia*) give no indication of any similar ability.

Euphausiacea

Of the eleven genera of euphausiaceans all ten in the Euphausiidae have complex photophores of similar structure and only in the monotypic family Bentheuphausiidae are they lacking. None produce a secretory luminescence. Most species have ten ventral photophores, a pair each on the eyestalks, anterior and posterior thorax, and a single median organ on each of the first four abdominal segments. Species of *Stylocheiron* lack the anterior thoracic and posterior three abdominal organs, leaving a total of five photophores. The luminescence of these animals was among the earliest of that to be recognized in Crustacea, despite the fact that the photophores were first described as accessory eyes, a misinterpretation reinforced by the fact that all the photophores except those in the eyestalk can be rotated.

Other modifications of the basic photophore pattern involve sexual dimorphism. In Atlantic species of *Nematobrachion flexipes* males lack the third abdominal organ and females the second and third (P. T. James, personal communication). Males of species of *Nematoscelis* may have one or more of the abdominal photophores enlarged. In *N. tenella, N. microps,* and *N. atlantica* there are three different male forms in each species. One has "normal" photophores and the other two have different enlarged photophores (Einarsson, 1942; James, 1973; Gopalakrishnan, 1975). In both *N. tenella* and *N. atlantica* the forms are similar but geographically separated. Where the two species overlap each occurs in a different male form. In general the photophore size in euphausiids is related to the body size, but in the large species of *Thysanopoda* (up to ~150 mm) the photophores are proportionally much smaller (Herring and Locket, 1978). These species have the greatest depth distribution.

The luminescence of free-swimming animals is generally steady, lasting for

periods of up to 36 min (e.g., Korte, 1964) and ventrally directed, but any disturbance can initiate a shorter flash with a lengthy decay (David and Conover, 1961; Kay, 1965). Luminescence is inhibited by O_2 saturations below 90% (Kils, 1979) and can be stimulated by exposure to light. Mauchline (1960) reported both seasonal and diurnal variations in the sensitivity to a photoflash. These light responses involve both inhibitory and excitatory components and blue light is the most effective stimulus (Kay, 1965, 1966). Tett (1969, 1972), who made a detailed study of the effects of temperature on the responses, also found seasonal changes in the responsiveness and suggested that luminescence was involved in spermatophore transfer behaviour. Luminescence can also be stimulated by a number of drugs, including serotonin (5H-T), bufotenin, and LSD, subthreshold doses of which will facilitate the flash-stimulated responses (for references see Herring and Locket, 1978).

Paired photophores usually luminesce in synchrony but the three groups may be illuminated independently. The ocular photophores are often the brightest and are usually the first to develop, appearing in the third calyptopis larva (Pierantoni, 1921). In *Meganyctiphanes* and *Euphausia* spp. the photophores develop in an anterior–posterior sequence and all may be visible by the third furcilia larva. This sequence does not apply to all species (Gopalakrishnan, 1973). The first photophores become functional in the later calyptopis larvae and one or more functional groups are present in the furcilia stages (e.g., Lapota and Losee, 1984). Pierantoni (1921) and Petersson (1968) have shown how the photophores develop from an epidermal thickening of undifferentiated cells to the complexity typical of the adult animal.

Recent electron microscope studies have described the organization of a typical photophore and its complex association with the blood vessels (Bassot, 1966a, b; Harvey, 1977; Herring and Locket, 1978). The photophore is enclosed in a red pigment layer, internal to which is a multilayer reflector probably composed of chitin. This encloses a group of large cells (A cells) traversed by capillaries which run to a central sinus. At their junction with the sinus they pass through a specialized sphincter formed of the C cells which contain contractile fibrils. Projecting into the central sinus are extensions of a third cell type (B cells) which form the central light-emitting "lantern" (Herring and Locket, 1978). This has a striated appearance since each B cell projection is formed of a dense refractile region, resulting in a series of radially arranged rodlike elements. These are quasi-crystalline in structure and are in direct contact with the blood in the central sinus. Isolated lanterns glow spontaneously. Beneath the lantern is a large biconvex lens (which is absent from the eyestalk photophores). Between the lens and the edge of the reflector is a lamellar ring formed of flattened cells aligned parallel to the optical axis of the photophore. The outer edge of the photophore is covered by large translucent cap cells.

Nerve fibres are associated with the blood vessels; their terminations have been observed only on the C cells. It seems likely that luminescence is controlled by the activity of the C cell sphincters on the blood supply to the lantern. Steady luminescence can be regarded as a steady state blood flow through the lantern. The excitatory effects of drugs could operate either centrally or peripherally (at the sphincter). The lens serves to collimate the light and the lamellar ring to intercept light that would emerge between the lens and reflector and reflect it closer to the optical axis. The resulting angular distribution of light from a live animal is very close to that of ambient downwelling light in the sea (Herring and Locket, 1978).

The ventral photophores can be rotated in unison in the sagittal plane by a

system of connecting ligaments and antagonistic muscles (Hardy, 1962, 1964). The rotation is coupled to movements of the eyes through a maximum of 180°; the eyes track a light source (e.g., that from the surface) and the consequence is that the photophores will always be directed downwards regardless of changes in the orientation of the body (Land, 1980). This fact, allied to the reduced size of photophores in the deepest species and the match in the angular and spectral distribution of the emitted light with that in the sea, suggests that their primary role is that of a counterillumination camouflage system (Clarke, 1963). This need not be their only role but there are insufficient behavioural data to identify other functions with certainty.

Decapoda

In marked contrast to the uniformity of luminescence in euphausiids is the variety of photophore structure and expression in the decapods. There is undoubted luminescence only in certain pelagic shrimps and prawns, largely in the deep-sea species. It may appear in three distinct forms: (1) a luminous secretion from the oral region, (2) superficial cuticular photophores on the body and limbs, and (3) internal photophores formed from modified hepatopancreas tubules. Different species have either cuticular or hepatic photophores, but never both. Some species producing a luminous secretion may also have photophores of either type.

The production of a luminous secretion is a dramatic response, appearing as a pair of jets in the exhalant current, much like the mysid *Gnathophausia.* This behaviour not only provided the first account of a luminous decapod (*Thalassocaris,* by Dana, 1852) but is also the commonest form, has been encountered by observers in submersibles (e.g., Beebe, 1926), and can be repeatedly elicited from captive animals. It occurs in all the genera of the Oplophoridae, in the pandalids *Heterocarpus* and perhaps *Plesionika,* the pasiphaeid *Glyphus,* the thalassocaridid *Thalassocaris,* and in one penaeid, *Plesiopenaeus* (references in Herring, 1976). The secretion may be quite viscous and retain its luminosity for many minutes, or may be more fluid with a rapid decay. Earlier observers believed it to be derived from the "green glands" or "cuticular glands" but it is more likely to be a hepatic product regurgitated from the mouth (Herring, 1976). It is always associated with a hepatopancreas which is luminescent if macerated. The secretion is probably a defensive response and can sometimes be elicited with a flashlight (Herring and Barnes, 1976).

Hepatic photophores are limited to *Thalassocaris, Chlorotocoides, Parapandalus,* and *Sergestes.* In the former three genera there are four photophores, one at each ventral corner of the hepatopancreas. In *Sergestes* (where they are known as the organs of Pesta) the anterior pair is similarly situated but posteriorly there may be additional groups of luminous tubules less clearly contained in a single photophore and with differences in their arrangement (Foxton, 1972). Luminous tubules of *Sergestes* have a blue distal (ventral) tip, a central region whose cells contain paracrystalline luminescent particles, and a proximal region of cells containing microspheres which act as a diffuse reflector. The lumen is continuous with that of the normal hepatic tubules. The paracrystalline material is fluorescent and glows spontaneously when isolated. In the thalassocaridids and *Parapandalus* the modified tips of several tubules are aggregated into each photophore and the reflector and pigment layer surrounds the entire group (Dennell, 1940; Latz and Case, 1980; Herring, 1981b).

Some, at least, of the organs of Pesta can be rotated (Omori, 1974). Detailed studies of *Sergestes similis* have shown that both the eyestalk and posterior light

organ are capable of 140° of compensatory movement during pitch body tilt, maintaining the organs horizontally (Latz and Case, 1982). These responses are statocyst-mediated and in most circumstances are closely coupled. No studies have been undertaken on the other genera with hepatic photophores, but changes in the orientation of photophores of *Parapandalus* suggest that they, too, are capable of some rotation.

Cuticular photophores are present in the oplophorid genera *Systellaspis* and *Oplophorus* (as well as a luminous secretion), in several species of the deep-water sergestid *Sergia,* and in certain species of the solenocerids *Hadropenaeus, Hymenopenaeus, Mesopenaeus,* and *Solenocera* (Burkenroad, 1937; Perez Farfante, 1977; A. J. Bruce, personal communication). They are present on the carapace, abdomen, and appendages, and range in number from six in *Hymenopenaeus debilis* to 150–160 in some species of *Sergia* and *Systellaspis* (e.g., Kemp, 1910; Terao, 1917; Omori, 1969). Their distribution shows sexual dimorphism in *Sergia robustus* and *S. richardi* (Dennell, 1955). Almost all the photophores are directed ventrally, even those on the limbs when they are folded in the normal swimming position. In the oplophorids and some species of *Sergia* they are associated with a blue pigmentation of the overlying cuticle. In other *Sergia* species they appear as carmine spots (Dennell, 1955). Tissues covered by a bluish cuticle are present in similar positions in *Gennadas* spp., but luminescence has not been observed in this genus.

The structure of the cuticular photophores of *Systellaspis* and *Oplophorus* have been most recently studied by Dennell (1940) who has shown that there are morphological differences both in different regions of the same species and between species, though most photophores are derived from groups of similar photogenic units (=photocytes) with associated pigment, reflector, and lenslike structures. The cuticular photophores of *Hymenopenaeus* were studied by Ramadan (1938) and of *Sergia* by Terao (1917) and Dennell (1940). Some species of *Sergia* have thick cuticular lenses (e.g., *S. challengeri*) but in others these are lacking (e.g., *S. regalis*). Dennell (1940) describes the photogenic region in *S. regalis* as containing rodlike elements in a fibrous matrix.

Few observations of in vivo luminescence have been made on species with cuticular photophores (Herring, 1976). *Systellaspis* and *Oplophorus* species respond to 5H-T with a steady luminescence. Various reports of active luminescence in *Sergia* describe only a steady glow or irregular flashes (e.g., Dennell, 1955). Observations on species with hepatic photophores are similarly limited, with the notable exception of *Sergestes similis.* In this species a series of elegant experiments have shown that the animal can luminesce steadily for long periods, that it can adjust the intensity of its light output to match both long and short term changes in the overhead light, and that covering the eyes abolishes the light-matching response (Warner *et al.,* 1979; Warner, 1981). The angular distribution of its light closely matches that in the sea, as does that of *Oplophorus* and *Systellaspis* (Herring, 1976).

All these data, combined with the fact that the spectral emission of photophores of *Sergestes similis* and *O. spinosus* matches that of ambient light in the sea (see below), provide strong support for the supposition that the ventral cuticular and hepatic photophores are employed as a counterillumination camouflage (Warner *et al.,* 1979). Less certain is the relative effectiveness in such a role of the few ventral photophores in the near benthic solenocerids, some of which are rather shallow-living species. The role of sexually dimorphic photophores is as much a matter for conjecture as in the euphausiids. Additional circumstantial evidence

for a camouflage function for the photophores derives from their depth distribution. In general those species with photophores have their daytime adult population maxima at mesopelagic depths of <900 m, i.e., are still potentially subject to ambient light from the surface (Foxton, 1970). The blue pigments probably act as appropriate spectral filters (Denton *et al.,* in press). Species of *Systellaspis* in the Atlantic provide a clear illustration. *Systellaspis debilis* and *S. pellucida* are relatively shallow (mesopelagic) species with many prominent photophores. *Systellaspis cristata* is a deeper species and has only a few small photophores (which are more prominent in the shallower-living juveniles), and *S. braueri,* the deepest species, lacks photophores altogether. In contrast, species from all depths can produce a luminous secretion.

The developmental sequence of the photophores has been described by Coutière (1906) for *Systellaspis debilis* and they are visible in the earliest larvae. Development is similar in *Oplophorus spinosus* and in species of *Sergestes* the organs of Pesta first appear at the mastigopus stage (Gurney and Lebour, 1940).

There are several reports of luminescence in other species, either from an indeterminate source, e.g., *Leptochela* (Chace, 1940), *Parapasiphaea* (Widder *et al.,* 1983), or as organs speculatively suggested as luminous, e.g., *Hypsophrys* (Williams, 1976). Other reports have been listed previously (Herring, 1976). While it is likely that luminescence remains undiscovered in other species, such unconfirmed reports should not be accepted without more detail. Even visible luminescence need not be a guarantee of a normal capability, as illustrated by cases of bacterial infection or the ghost crab luminescence caused by eating luminous ostracods (Felder, 1982).

General Aspects

Physicochemical Features

The few physical data available for crustacean luminescence are limited to the angular distribution, intensity, and spectral emission of the light. The latter factor has been mentioned above in relation to the functions of decapod and euphausiid photophores. Intensity measurements have been made on very few species and must necessarily be regarded as minimum levels. Reported values range between 10^{-4} and 10^{-7} μW cm^{-2} at 1 m (e.g., Boden and Kampa, 1974; Herring, 1976, 1981a; Warner *et al.,* 1979) with copepods giving surprisingly high recorded intensities in one investigation (Filimonov and Chumakova, 1969). Warner *et al.* (1979) have shown that the values for *Sergestes similis* accord with a counterillumination hypothesis in that they are equivalent to those it would normally experience in the sea.

Emission spectra have been reported for a variety of crustaceans in several recent publications (Swift *et al.,* 1977; Biggley *et al.,* 1981; Widder *et al.,* 1983; Herring, 1983). The last paper includes a listing of data for almost all species reported up to that time. It is noteworthy that those species with potentially counterilluminating photophores (euphausiids and decapods) have relatively narrow bandwidth emissions with maxima at 470–475 nm, very similar to that of light in clear oceanic water. Secretory responses have a generally broader bandwidth and emission maxima ranging from 455 to 490 nm. The marked differences between the spectra of the photophores and secretion of *Oplophorus spinosus* are commensurate with these general characteristics. Calanoid copepods and *Gnathophausia* have greener emissions than ostracods and decapods. The photocytes of *Oncaea* and *Scina,* however, have much shorter wavelength emission maxima

around 435 nm (a difference noted in 1895 by Giesbrecht). The more general significance of spectral differences has been discussed elsewhere (Herring, 1983). There is no information on whether any photophore luminescence is polarized.

The chemical nature of the luciferin of crustaceans, and its origins, has received some recent attention. The luciferin of *Vargula,* the first of such marine compounds to be identified chemically, is derived from three amino acids, tryptophan, iso-leucine, and arginine. Precisely the same luciferin is present in several fishes and experimental evidence indicates that there is a dietary requirement for ostracod luciferin for luminescence in at least some fish populations (see Herring, 1982, for references). Subsequent studies have identified at least two other chemical systems in crustaceans. One, involving a luciferin similar to that of *Vargula* but derived from different amino acids, has been identified in the decapods *Oplophorus* and *Heterocarpus* (Inoue *et al.,* 1976; Shimomura *et al.,* 1978). This luciferin was originally identified in coelenterates and is also known as coelenterazine. It has also been identified in *Acanthephyra, Gnathophausia* (Cormier, 1978), *Systellaspis* and *Sergestes* (Shimomura *et al.,* 1980), and the copepod *Pleuromamma* (McCapra and Hart, 1980) as well as in a number of fishes and squids. The third system is limited to the euphausiids and appears to be based upon a tetrapyrrolic compound which is very similar to that in dinoflagellate luciferin (Shimomura, 1980; Dunlap *et al.,* 1980, 1981). The possibility of a dietary link between the luciferins of the two groups cannot be discounted but seems intuitively improbable as the *sole* source of euphausiid luminescence. Nevertheless, recent studies by Frank *et al.* (1984) have shown that dietary sources can replenish the luciferin supply (and luminescence) of specimens of *Gnathophausia* whose luminescent system has previously been exhausted. The effectiveness of crustaceans such as *Sergestes* and the copepod *Gaussia* in reinitiating luminescence in these experiments indicates that they, too, probably have coelenterazine as their luciferin. Whether such a dietary source is essential for *Gnathophausia* is a fascinating but unresolved problem. Interestingly the spectral emission of specimens of *Gnathophausia* which were fed luciferin of *Sergestes* or *Gaussia* was typical of normal *Gnathophausia,* not that of the prey, indicating that the luciferin was not the spectral determinant. Preliminary attempts to demonstrate in *Oplophorus* in vivo biosynthesis of coelenterazine from ^{14}C tyrosine (one of its component amino acids) have failed to demonstrate any label incorporation (McCapra and Herring, unpublished).

There are, then, at least three chemical systems in the Crustacea. The euphausiid system is limited to that order and the system of *Vargula* to the ostracods. It may even be restricted to the Cypridinidae for it has not been possible to demonstrate cross-reactions between luciferins and luciferases of *Vargula* and *Conchoecia* (Campbell and Herring, unpublished). The coelenterazine system extends at least to the copepods, mysids, and decapods, but the position of the amphipods is unresolved.

The Significance of Crustacea in Sea-surface Luminescence

Dinoflagellates have generally been regarded as the major cause of sea-surface luminescence, but the contribution of some of the smaller zooplankton is being increasingly recognised (e.g., Swift *et al.,* 1983). The dense aggregations of ostracods present in the northern Indian Ocean provide one dramatic example (Tett and Kelly, 1973; Daniel and Jothinayagam, 1977, 1979). Copepods are less frequently reported as major sources of surface luminescence but they have been

implicated in general in the Red Sea and Sargasso Sea (Rudjakov and Voronina, 1967; Swift *et al.*, 1983). Dense concentrations of *Metridia lucens* may produce intense surface luminescence in northern European waters (Farran, 1903) and I have observed similar effects off the northwest African coast produced by *Pleuromamma piseki*. Euphausiid luminescence at the surface usually takes the form of patches of milky white luminescence (Tizard *et al.*, 1885; Ivanov, 1969). There are no reports of widespread luminescence produced by decapods, though local phenomena may be produced by some of the shallower species (Herring and Barnes, 1976). References to other examples of crustacean luminescence may be found in Tarasov (1956) and Hickman *et al.* (1980). The luminescence of these crustaceans has some commercial applications insofar as it may be used as an indicator of shoal size when observed from the air using image intensifiers. The luminescence of both *Metridia* and *Nyctiphanes* has been used to follow shoals of pilchards and cape hake (Cram, 1973; Cram and Schulein, 1974) and it has been suggested that the technique might aid assessment of the Southern Ocean krill stocks (Cram and Malan, 1977).

General Considerations and Future Research

One of the apparently perplexing aspects of crustacean luminescence is its sporadic distribution, a feature common to many other major groups. In taxonomic terms it is a rare attribute. Only about 1% of the 5,354 recognised genera (Bowman and Abele, 1982) contain luminous species (Table 1). At the ordinal level the number of luminous species is greater than 1% only in myodocopid and halocyprid ostracods, calanoid copepods, and Euphausiacea. The relevance of this type of accounting is that bioluminescence is an attribute developed in response to ecological pressures and not an inherent property of an archetypal crustacean that has endured through the ramification of the group. Though its morphological connotations (photophores, etc.) may be of systematic convenience (as in many other groups), I am convinced that in general they tell us much more about their owners' relationship to their environment than they do about their relationships to each other. At best they are highly apomorphic characters (Hessler *et al.*, 1982).

The pelagic environment is clearly the main spur to the employment of bioluminescence, whether at night near the surface or continuously in the darkness of the deep sea. This is reflected among the decapods, for example, in the high proportion of luminous individuals and species in the oceanic fauna (Herring, 1976). Is the successful exploitation of the pelagic environment by the Oplophoridae due in some measure to the acquisition of luminescence by an ancestral species? If so, was it after the separation of the other atyoid families or have they subsequently lost it? Has hepatic luminescence been independently evolved in the caridean families and the Sergestidae, despite involving the same luciferin? Hastings (1983b) recognised three separate evolutionary origins of bioluminescence in the Crustacea, based on the chemistry of the systems, but either this must be an overly conservative estimate or the phylogenetic basis of the current classification system is seriously awry.

If luminescence tells us more about environmental pressures than about ancestry we need equally to accept that it highlights the inadequacies of our concepts of oceanic niches. The extensive and elaborate luminescence of *one* species of *Oncaea* should be an important guide to some differentiating feature of its niche separation. We cannot yet read the message in the guide.

A comparison of crustacean bioluminescence with that of other arthropods shows that there is little common ground with that in the chilopods, diplopods,

Table 1. Distribution of crustacean genera of known luminescence (following the classification of Bowman and Abele, 1982). Genera whose luminescence is more doubtful are noted in the text.

Class	Subclass	Order	Family	Genus
Cephalocarida				None
Branchiopoda				None
Remipedia				None
Maxillopoda	Mystacocarida			None
	Cirripedia			None
	Copepoda	Calanoida	Augaptilidae	*Augaptilus, Centraugaptilus, Euaugaptilus, Haloptilus, Heteroptilus, Pachyptilus*
			Lucicutiidae	*Lucicutia*
			Heterorhabdidae	*Heterorhabdus, Hemirhabdus, Heterostylites, Disseta*
			Metridiidae	*Metridia, Pleuromamma, Gaussia*
			Megacalanidae	*Megacalanus*
		Harpacticoida	Aegisthidae	*Macrosetella, Aegisthus*
		Cyclopoida	Oithonidae	*Oithona*
			Oncaeidae	*Oncaea*
		Poecilostomatoida		None
		Siphonostomatoida		None
		Monstrilloida		None
		Misophrioida		None
		Mormonilloida		None
	Branchiura			None
Ostracoda	Myodocopa	Myodocopida	Cypridinidae	*Cypridina, Vargula*
		Halocyprida	Halocypridae	*Conchoecia*
	Podocopa			None
	Palaeocopa			None
Malacostraca	Phyllocarida			None
	Hoplocarida			None
	Eumalacostraca	Bathynellacea		None
		Anaspidacea		None
		Thermosbaenacea		None
		Spelaeogriphacea		None
		Mysidacea	Lophogastridae	*Gnathophausia*
		Amphipoda	Lysianassidae	*Cyphocaris, Thoriella, Danaella, Chevreuxiella*
			Scinidae	*Scina, Acanthoscina*
			Lanceolidae	*Scypholanceola, Megalanceola*
			Pronoidae	*Parapronoe*
		Isopoda		None
		Tanaidacea		None
		Cumacea		None
		Euphausiacea	Euphausiidae	*Euphausia, Meganyctiphanes, Nyctiphanes, Nematobrachion, Nematoscelis, Pseudeuphausia, Stylocheiron, Tessarabrachion, Thysanoessa, Thysanopoda*

Table 1. Continued.

Class	Subclass	Order	Family	Genus
		Amphionidacea		None
		Decapoda	Solenoceridae	*Hymenopenaeus, Hadropenaeus, Mesopenaeus*
			Sergestidae	*Sergia, Sergestes*
			Oplophoridae	*Acanthephyra, Ephyrina, Hymenodora, Meningodora, Notostomus, Oplophorus, Systellaspis*
			Pasiphaeidae	*Glyphus*
			Pandalidae	*Heterocarpus, Parapandalus*
			Thalassocarididae	*Chlorotocoides, Thalassocaris*

pycnogonids, and insects. Indeed, bioluminescence could be used to support the argument for a polyphyletic origin of the arthropods, except that the same criterion would lead to the interpretation of the Crustacea as a heterogeneous group. Chemically the only common factor is the probable involvement of the tetrapyrroles in diplopods and euphausiids (Shimomura, 1984), but the relationship is no closer than that between euphausiids and dinoflagellates—except that millipedes do not eat dinoflagellates!

The choice of areas most appropriate for future work must necessarily be personally biassed. I believe that there are three accessible areas which are likely to be profitable and of scientific merit. First, the clear establishment of precisely which zooplanktonic species are luminescent and their significance; second, an investigation of the chemical systems present in those crustaceans that have not yet been examined; and third, the pursuit of evidence for, or against, the biosynthesis of luciferin by particular species or its acquisition in the diet. All these are achievable goals, building on data already available. Less realistic in the short term is the hope that more behavioural studies of captive animals (or even better in situ) will be undertaken to try to establish the normal employment and importance of luminescence in the ecology of as wide a range of species as possible. Preserved corpses are an inadequate substitute for field observations or experimental manipulations.

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