Light emission

- **Photons in the visible range are emitted when electrons drop from an excited state to a lower energy state**
- **Visible spectrum extends from about 400 to 700nm**
- **Visible range photons contain a lot of energy, enough to do chemical work (or damage). For example energy of a mole of photons in the visible is about 50 kcal, compared to about 7 for hydrolysis of a mole of ATP**

Types of light emission

- **Incandescence**
  - Excited states produced by thermal energy
- **Fluorescence**
  - a photon is absorbed, elevating an electron to a higher energy state
  - Electron drops to ground state, emitting a photon
  - Fast and efficient, often mistaken for bioluminescence
- **Phosphorescence**
  - Special case of fluorescence
  - Energy transfer between electrons before photon emission
  - Slow

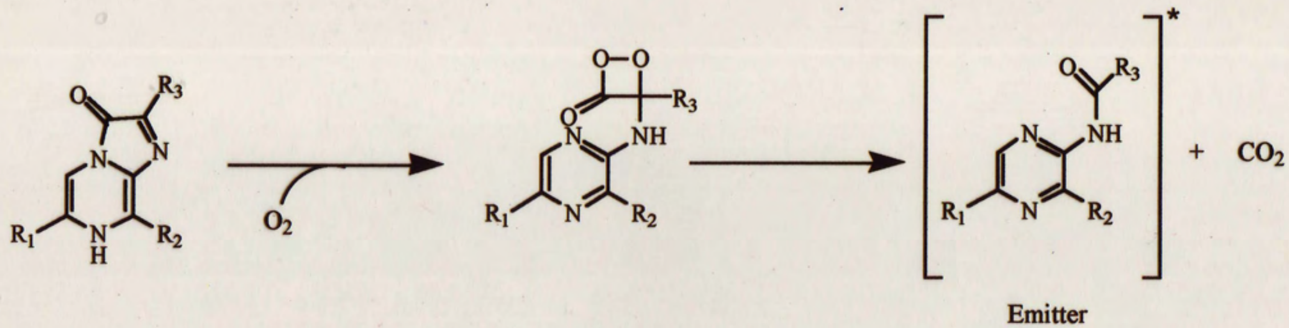
Chemiluminescence

- **Chemical reaction provides energy**
  - **Most chemical reactions don't provide enough energy (> 50 kcal/mole)**
- **Requires a compound with a suitable electron to give the excited state**
- **Major types**
  - **Singlet O_2**
  - **Electron transfer to give excited state**
  - **Decomposition of peroxides**
    - **Only type known in bioluminescence**

Bioluminescence

- A special case of chemiluminescence
- Substrate = luciferin, enzyme = luciferase
- $O2$ always involved: luciferases are oxygenases
- Color: 450 to 600
  - Color can be modulated by
    - Changes in luciferase
    - Secondary emitters
      - Energy transfer
      - Photon absorption and re-emission
  - Intensity
    - $10^{-3} – 10^{-9}$ μW/cm^2 ($10^9 – 10^3$ quanta/s)

Typical Bioluminescence Reaction: Imidopyrazine



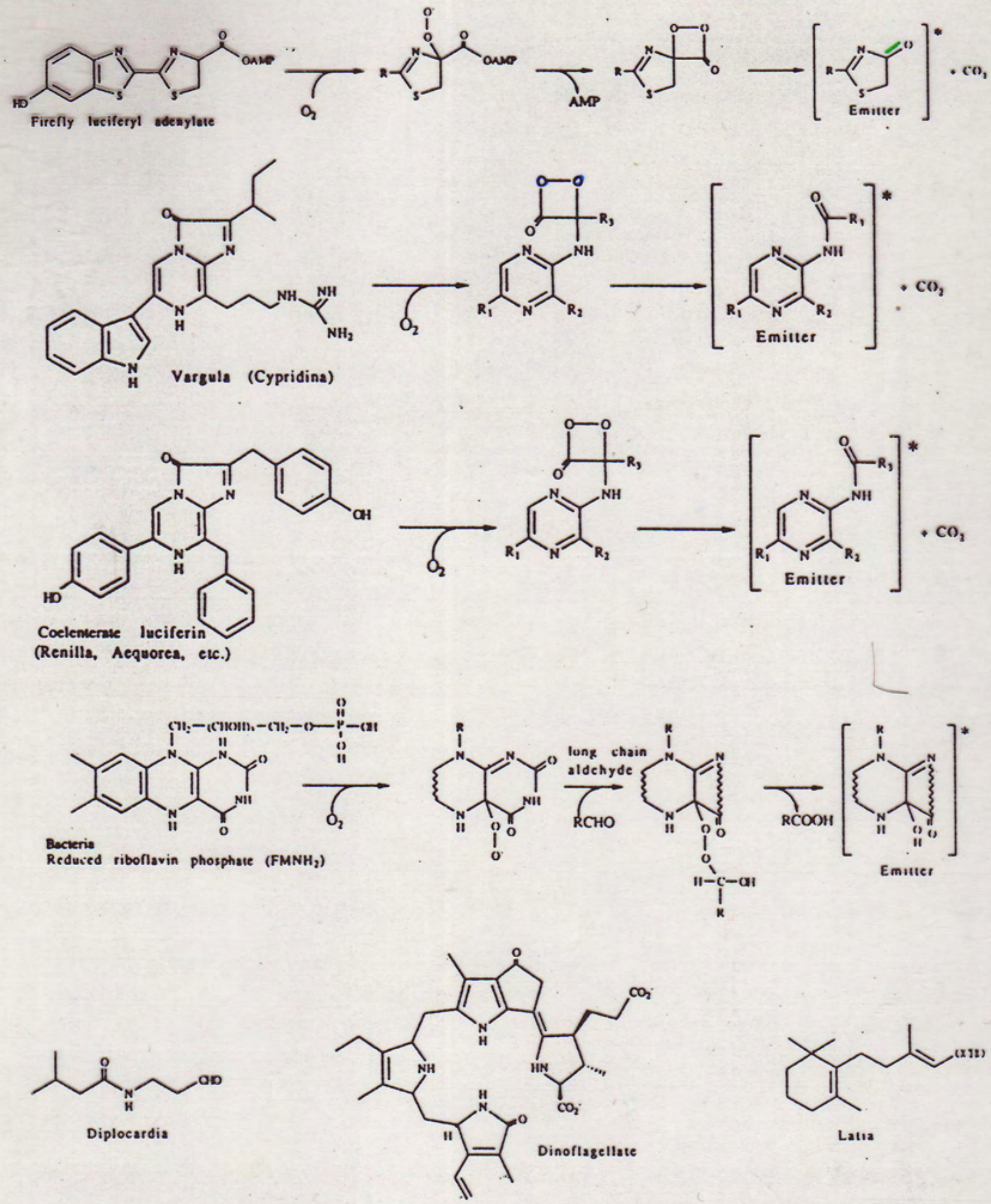


Figure 1. Structures of different luciferins, oxygen containing intermediates, and postulated emitters.

Firefly luciferin

- reacts with ATP to form luciferyl adenlyate, which reacts with oxygen
    - forms four-member ring peroxide, decomposes to release CO_2 and leave excited carbonyl emitter
    - confined to insects, not found elsewhere
- Because ATP is required to activate the luciferin the reaction has long been used as a sensitive assay for ATP

Vargula (Cypridina)

- imidazopyrazine nucleus
- ring peroxide mechanism
- found in ostracodes and several fishes

Coelenterazine

- imidazopyrazine
- ring peroxide
- found in
  - Cnidarians
  - Ctenophores
  - Crustaceans
  - molluscs (cephalopods)
  - fishes

Dinoflagellate

- linear tetrapyrrole – probably derived from chlorophyll
- product has an additional carbonyl group, but mechanism unknown
- found in dinos and euphausids (slightly modified)

Other luciferins

- **Annelids**
  - N-iso-valeryl-3-amino propanal
  - Unusual in that it uses H_2O_2 as the oxidant rather than O_2
  - mechanism unknown
  - occurs only in annelids
- **Latia**
  - mechanism unknown
  - only in the gastropod Latia

Frontier Areas

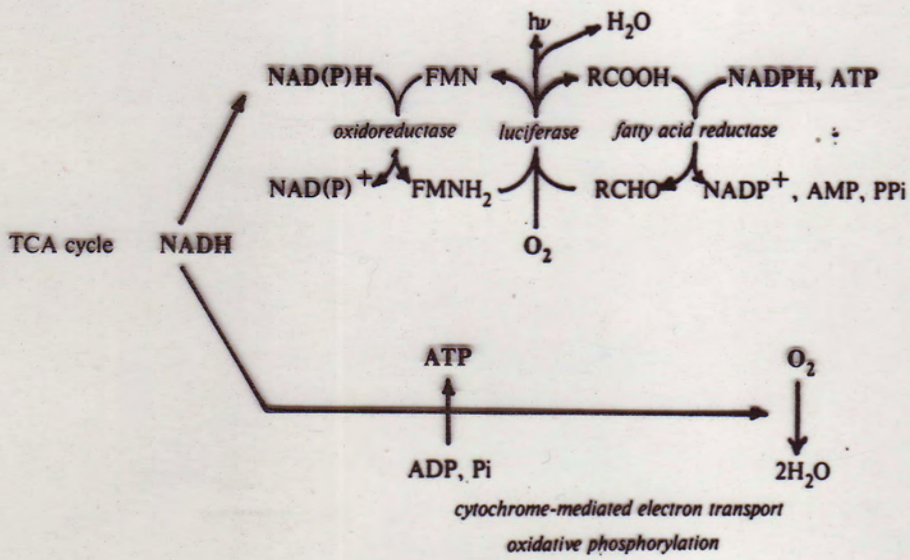
- **many unknown luciferins and mechanisms**
- **multiplicity of systems, many independent evolutionary origins**
- **repeated appearance of luciferins (esp coelenterazine) across taxa**
  - **lateral transfer, dietary or genetic**
  - **midwater organisms have to cope with and detoxify a lot of coelenterazine from their diet**
  - **accumulates in liver**
  - **may be fairly easy for detoxifying enzymes to become luciferases**
  - **wide open area for study of coelenterazine luciferase genes**

Bacteria

- lacks a classic luciferin
- forms a linear peroxide with flavin mononucleotide and aldehyde, no release of CO_2
- found only in bacteria, but accounts for luminescence in nematodes, cephalopods and fish as well

BACTERIAL BIOLUMINESCENCE PATHWAY

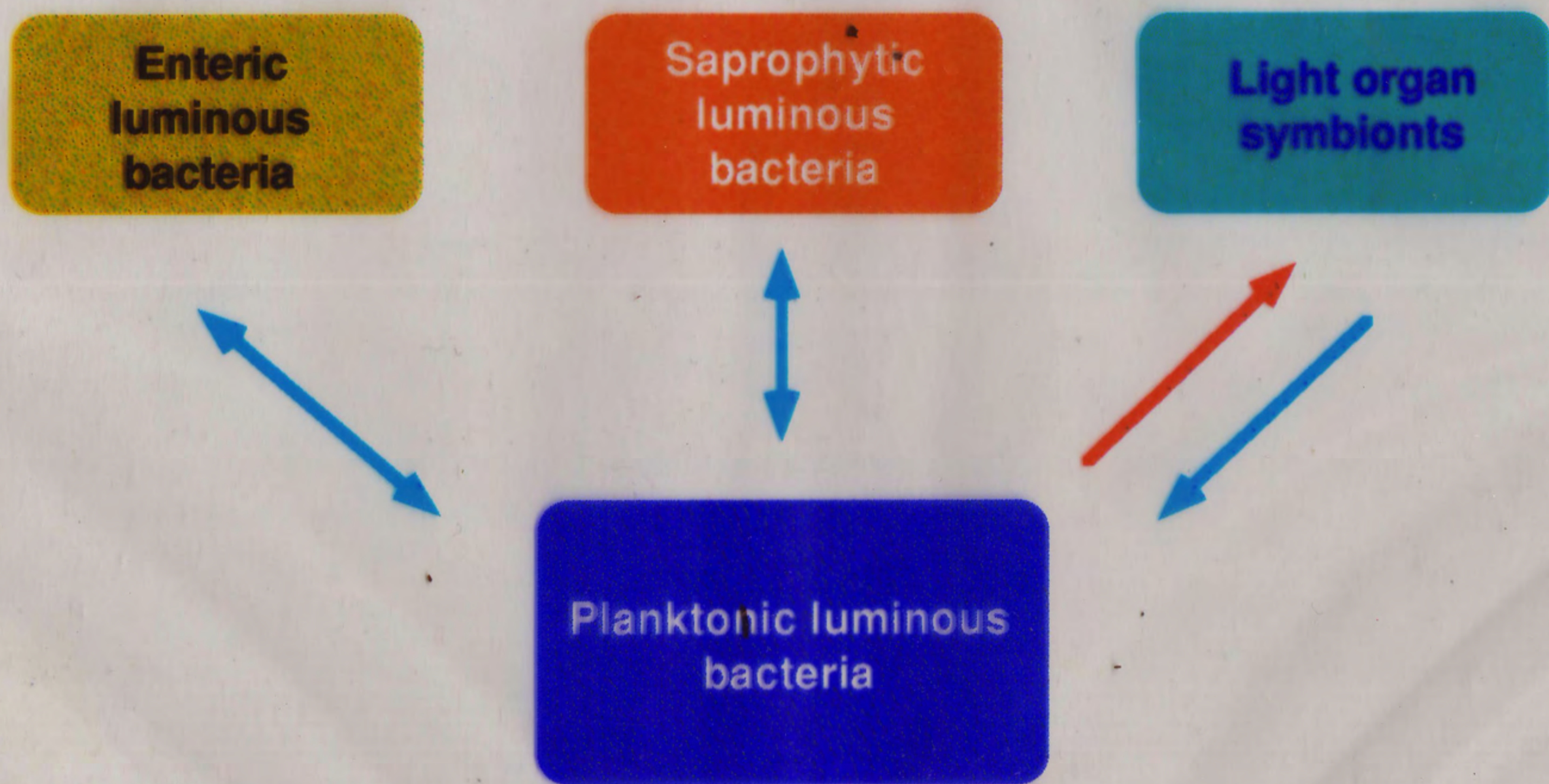
$$RCHO + FMNH_2 + O_2 \xrightarrow{luciferase} RCOOH + FMN + H_2O + h\nu$$



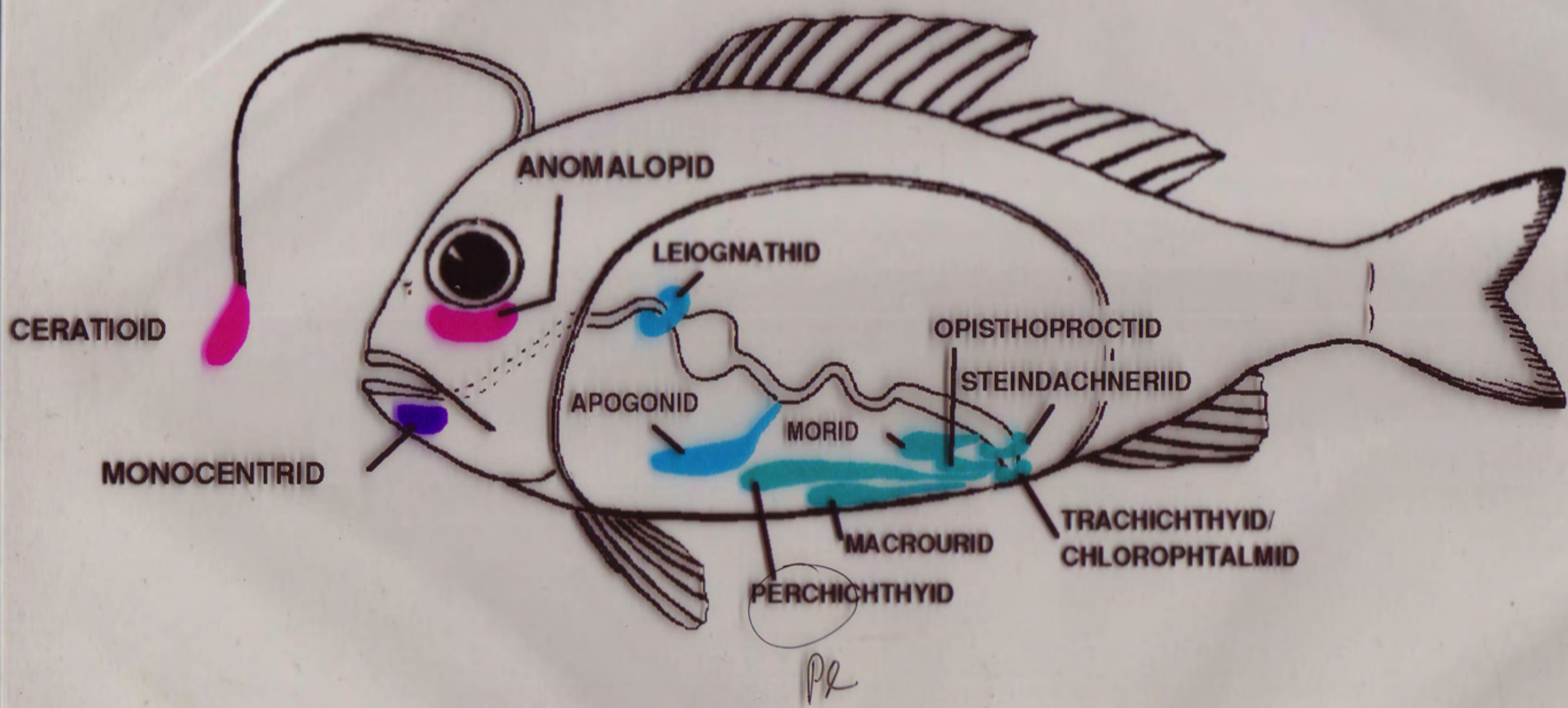
Total Energy Equivalents Required per Photon:

oxidoreductase	NAD(P)H
fatty acid reductase	NADPH
	ATP -> AMP, PPi
	2NADH, 2ATP

Habitats of Luminous Bacteria



Fish Light Organ Symbioses



Bacterial symbionts

Unculturable	*P. leiognathi*
V. fischeri	*P. phosphoreum*

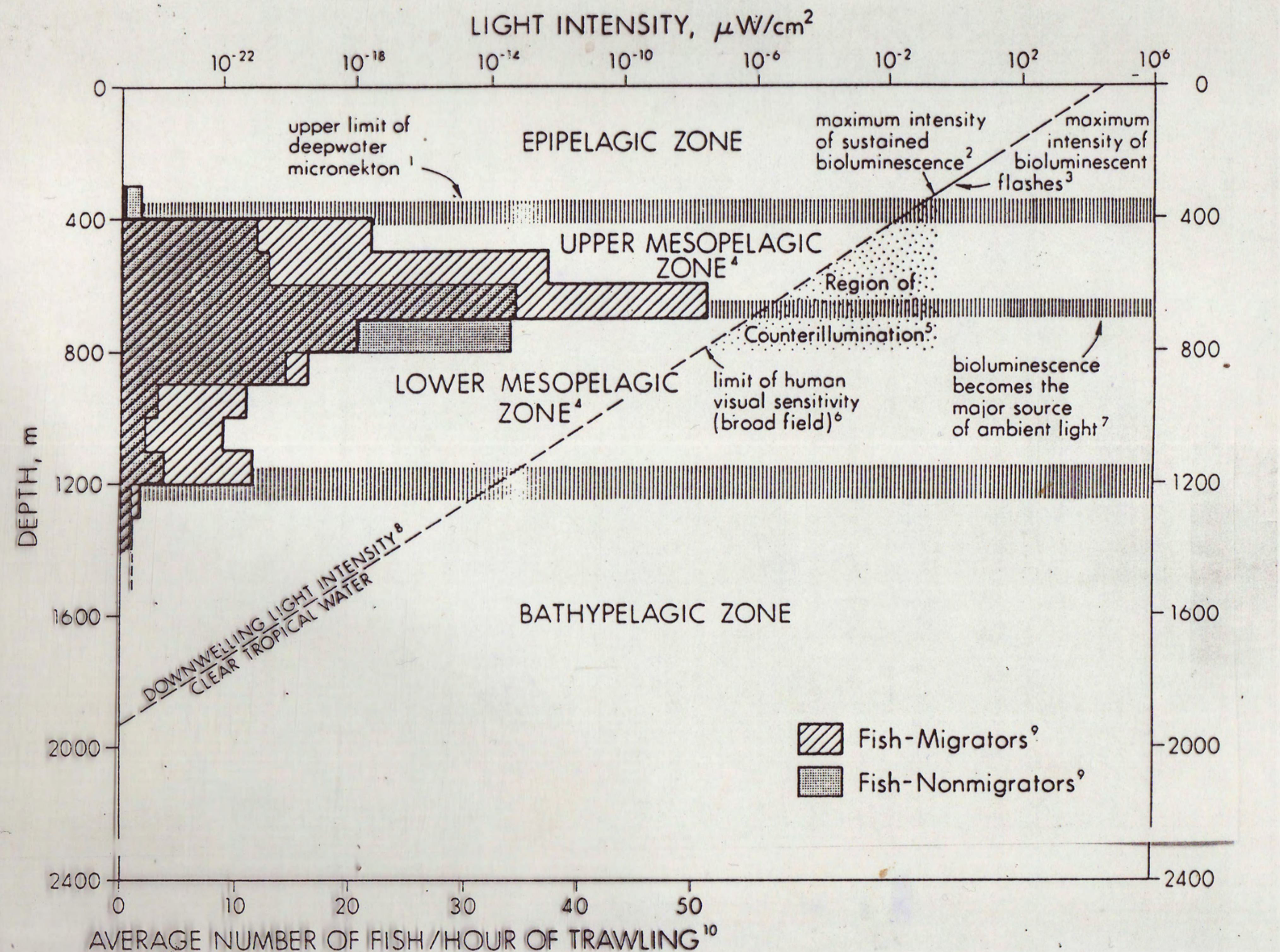

LIGHT INTENSITY, μW/cm²
10⁻²² 10⁻¹⁸ 10⁻¹⁴ 10⁻¹⁰ 10⁻⁶ 10⁻² 10² 10⁶
DEPTH, m
0 400 800 1200 1600 2000 2400
upper limit of deepwater micronekton 1
EPIPELAGIC ZONE
maximum intensity of sustained bioluminescence 2
maximum intensity of bioluminescent flashes 3
UPPER MESOPELAGIC ZONE 4
Region of Counterillumination 5
limit of human visual sensitivity (broad field) 6
bioluminescence becomes the major source of ambient light 7
LOWER MESOPELAGIC ZONE 4
DOWNWELLING LIGHT INTENSITY 8 CLEAR TROPICAL WATER
BATHYPELAGIC ZONE
Fish-Migrators 9
Fish-Nonmigrators 9
0 10 20 30 40 50
AVERAGE NUMBER OF FISH/HOUR OF TRAWLING 10

TABLE 1. Approximate Number and Proportion of Established Luminescent Taxa[a]

Taxon	Number of Luminescent Genera[b]	Number of Genera in Taxon	Percentage of Genera Luminescent	Representative Genera
Total (all organisms)	*666*	*/>100000*	*=~0.67*	
Bacteria	4	>246	~1.6	*Photobacterium, Vibrio*
Fungi	9	>802	~0.1	*Panus, Armillaria, Pleurotus*
Protista				
Dinoflagellata	11	>176	~6.3	*Gonyaulax, Noctiluca, Pyrocystis*
Radiolaria	9	>283	~3.2	*Thalassicola, Collozoum*
Animalia				
Cnidaria	65	1104	5.9	
Hydrozoa	37	381	9.7	*Obelia, Aequorea, Hippopodius*
Scyphozoa	4	70	5.7	*Pelagia, Atolla, Periphylla*
Anthozoa	24	647	3.7	
Octocorallia	21	220	9.5	*Renilla, Pennatula, Thourella*
Hexacorallia	3	427	0.7	*Parazoanthus, Epizoanthus*
Ctenophora	15	31	48	*Mnemiopsis, Beroe, Bollinopsis*
Nemertea	1	176	0.6	*Emplectonema*
Annelida	40	1300	3.1	
Polychaeta	26	1000	0.3	*Harmothoe, Odontosyllis, Chaetopterus, Polycirrus*
Oligochaeta	14	195	7.2	*Eisenia, Diplocardia*
Mollusca	75	3945	1.9	
Gastropoda	7	3083	0.2	
Opisthobranchia	3	327	0.9	*Phyllirrhoe, Kaloplocamus*
Pulmonata	4	1177	0.3	*Latia, Planaxis, Quantula*
Bivalvia	2	573	0.4	*Pholas, Rocellaria*
Cephalopoda	66	139	47	
Coleoidea	66	138	48	
Octopoda	3	38	7.9	*Japetella, Eledonella*
Sepioidea	6 + 5B	19	58	*Spirula, Euprymna, Heteroteuthis*
Teuthoidea	51	80	64	
Myopsida	4B	9	44	*Loligo, Doryteuthis*
Oegopsida	47	71	66	*Ommastrephes, Watasenia, Cranchia, Histioteuthis*
Vampyromorpha	1	1	100	*Vampyroteuthis*
Arthropoda	187	84600	0.22	
Chelicerata	1	6000	0.02	*Collosendeis*
Crustacea	57	5400	1.1	
Copepoda	17	1200	1.4	*Oncaea, Metridia, Pleuromamma*
Ostracoda	3	757	0.4	*Vargula, Cypridina, Conchoecia*
Malacostraca	37	3200	1.2	
Mysidacea	1	120	0.8	*Gnathophausia*
Amphipoda	8	840	1.0	*Scina, Parapronoe, Thoriella*
Euphausiacea	10	11	91	*Euphausia, Meganyctiphanes*
Decapoda	18	1200	1.5	*Sergestes, Oplophorus, Acanthephyra*
Uniramia	129	73600	0.18	
Diplopoda	3	1632	0.18	*Motyxia, Spirobolellus*
Chilopoda	5	303	1.7	*Orphaneus, Geophilus*
Insecta	121	71500	0.17	

TABLE 1. (*Continued*)

Taxon	Number of Luminescent Genera[b]	Number of Genera in Taxon	Percentage of Genera Luminescent	Representative Genera
Collembola	1	394	0.25	*Onychiurus*
Coleoptera	117	24800	0.5	*Photinus, Photuris, Pteroptyx*
Diptera	3	6033	0.05	*Arachnocampa, Orfelia*
Echinodermata	47	1126	4.2	
Crinoidea	3	164	1.8	*Annacrinus, Thallassometra*
Holothuroidea	16	154	10	*Galatheathuria, Scotoplanes, Kolga*
Asteroidea	12	300	4.0	*Plutonaster, Hymenaster, Brisinga*
Ophiuroidea	16	275	5.8	*Ophioscolex, Ophiosila, Amphipholis*
Hemichordata	3	16	19	*Ptychodera, Balanoglossus*
Chordata	200	8838	2.3	
Urochordata	3 + 3B	182	3.3	*Oikopleura, Cyclosalpa, Pyrosoma*
Vertebrata	194	8653	2.2	
Chondrichthyes	5	151	3.3	*Isistius, Etmopterus, Spinax*
Osteichthyes	189	3881	4.9	
Teleostei (43)[c]	189	3867	4.9	
Anguilliformes (1)	1 + 1B	147	1.4	*Saccopharynx, Lumiconger*
Clupeiformes (1)	1	68	1.5	*Coilia*
Salmoniformes (3)	18 + 3B	90	23	*Opisthoproctus, Searsia, Photostylu*
Stomiiformes (9)	53	53	100	*Argyropelecus, Malacosteus, Stomias*
Myctophiformes (2)	33	35	94	*Diaphus, Lampanyctus, Stenobrachius*
Aulopiformes (4)	5 + 1B	40	15	*Chlorophthalmus, Benthabella*
Batrachoidiformes (1)	1	19	5.3	*Porichthys*
Lophiiformes (10)	31B(2)[d]	64	48	*Oneirodes, Linophryne, Melanocetu*
Gadiformes (3)	18B	76	24	*Physiculus, Nezumia, Malacocephalus*
Beryciformes (3)	7B	39	17.9	*Photoblepharon, Anomalops, Cleidopus*
Perciformes (6)	11 + 5B	1367	1.2	*Leiognathus, Apogon, Siphamia*

[a]Numbers and examples of luminescent genera are taken from Herring (126, 132a) and more recent references; the classification scheme and the number of genera in each taxon are taken mostly from Parker (189).
[b]B = Number of genera with bacterial luminescence; all others have intrinsic luminescence.
[c]The number of families with at least some luminescent species is given in parentheses.
[d]Two genera possess both intrinsic and bacterial luminescence.

diverse bioluminescent systems differ, the terms luciferase (enzyme) and luciferin (substrate) must be prefixed by the relevant taxon: for example, bacterial luciferase or firefly luciferin. Common features of all systems are a requirement for molecular oxygen and the involvement of a reactive intermediate peroxy compound; indeed, all luciferases may be classed as oxygenases (106), in which a product molecule (P) is formed in an electronically excited state $[P]^*$. Its return to ground state results in emission of a photon in the visible range (~400–650 nm):

$$\text{luciferin} + O_2 \xrightarrow{\text{luciferase}} \text{peroxyluciferin} \longrightarrow [P]^* \longrightarrow P + h\nu$$

Luminescence in the blue (460 nm) corresponds to an energy of ~62 kcal/ein-

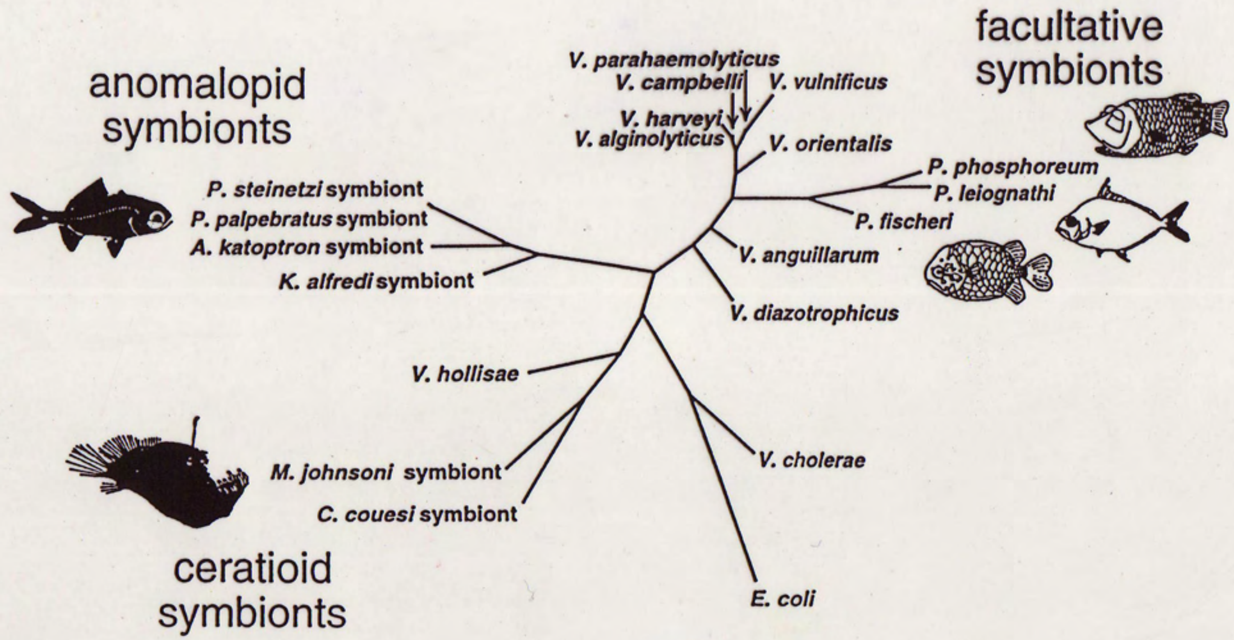


FIGURE 6. Phylogenetic relationships among luminous bacterial symbionts and other vibrios based on parsimony analysis of small subunit rRNA sequences. Representative hosts are illustrated next to their respective symbionts. (After Reference 20.)

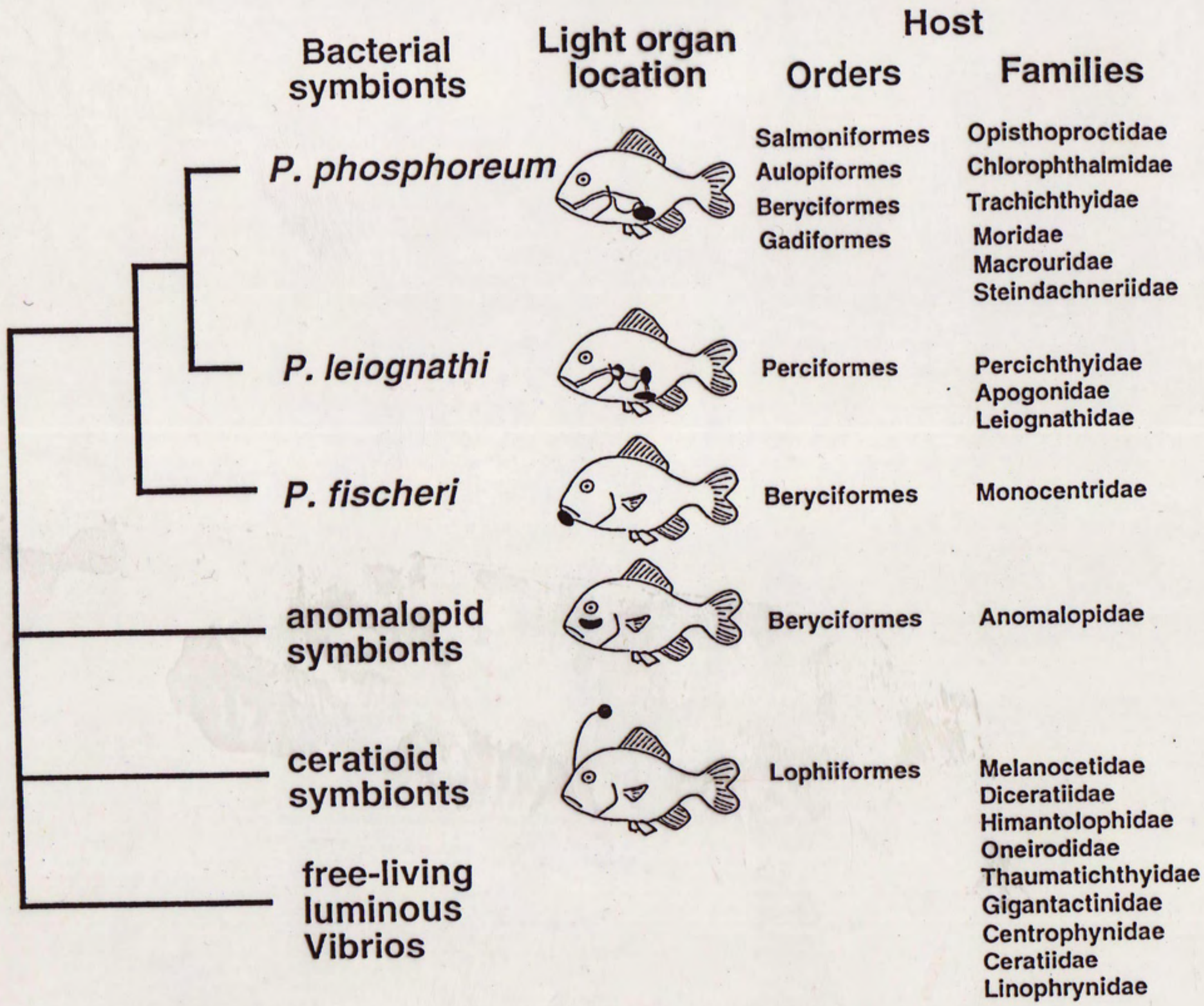


FIGURE 4. Phylogenetic relationships among light organ symbionts with illustration of light organ locations and listing of host associations.

Structure of an Anglerfish Esca

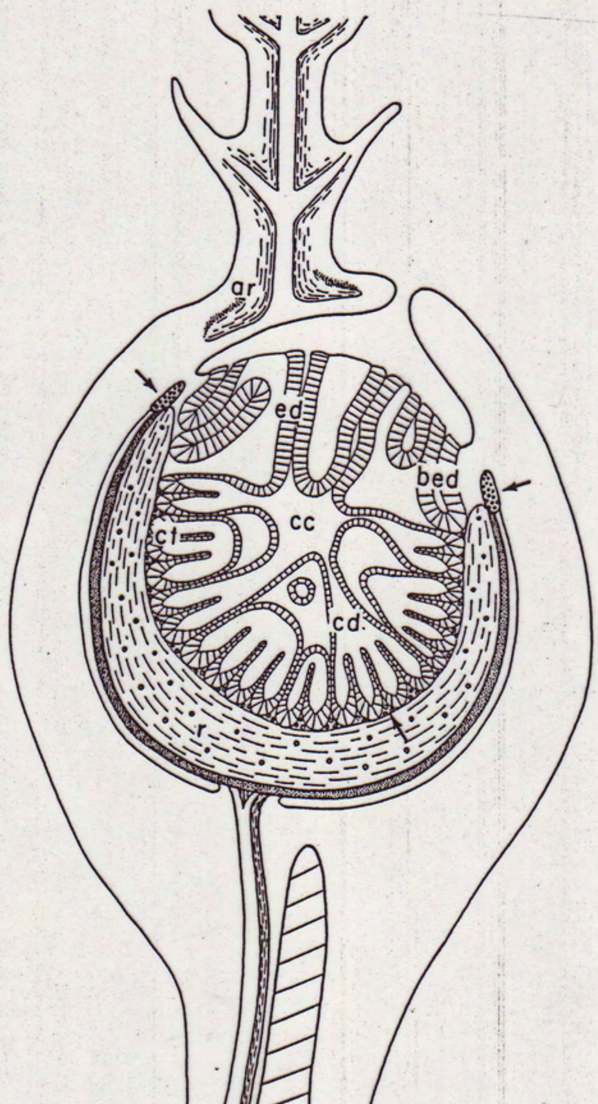
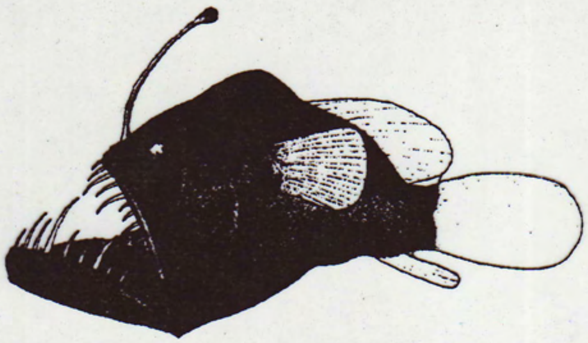
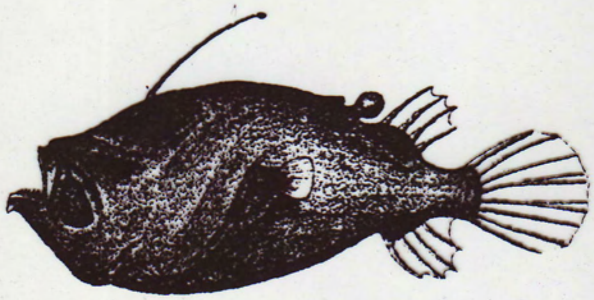


FIG. 4. Diagram of a vertical section through the esca of *L. arborifera*. Arrows indicate the position of smooth muscle fibres.



Melanocetus johnsonii



Cryptosarus couesi

Representative Ceratioids

Suborder Ceratioidei
10 Families
~ 80 species

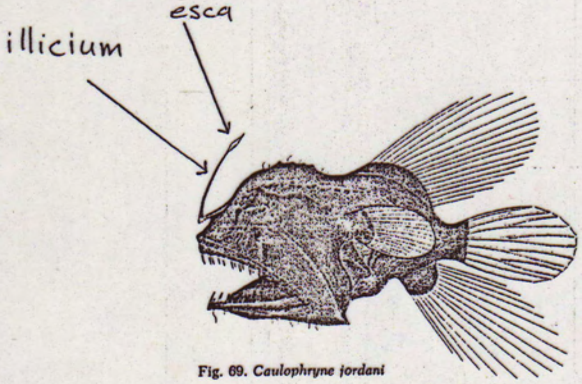


Fig. 69. *Caulophryne jordani*

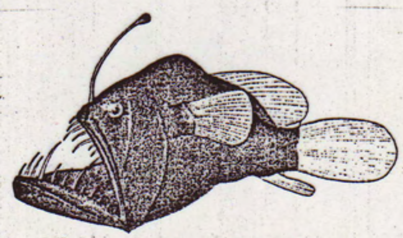


Fig. 70. *Melanocetus johnsonii*

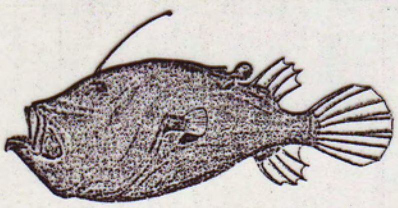


Fig. 71. *Cryptopsarus couesii*

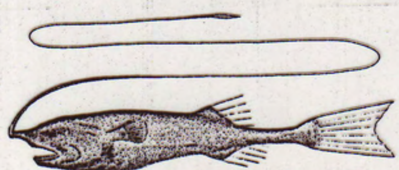


Fig. 74. *Gigantactis macronema*

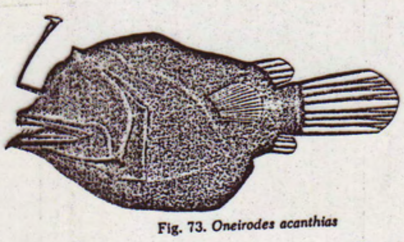
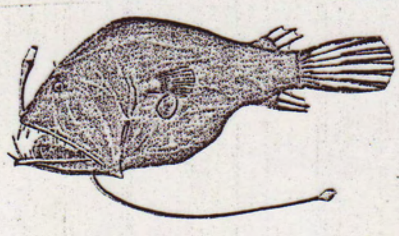


Fig. 73. *Oneirodes acanthias*



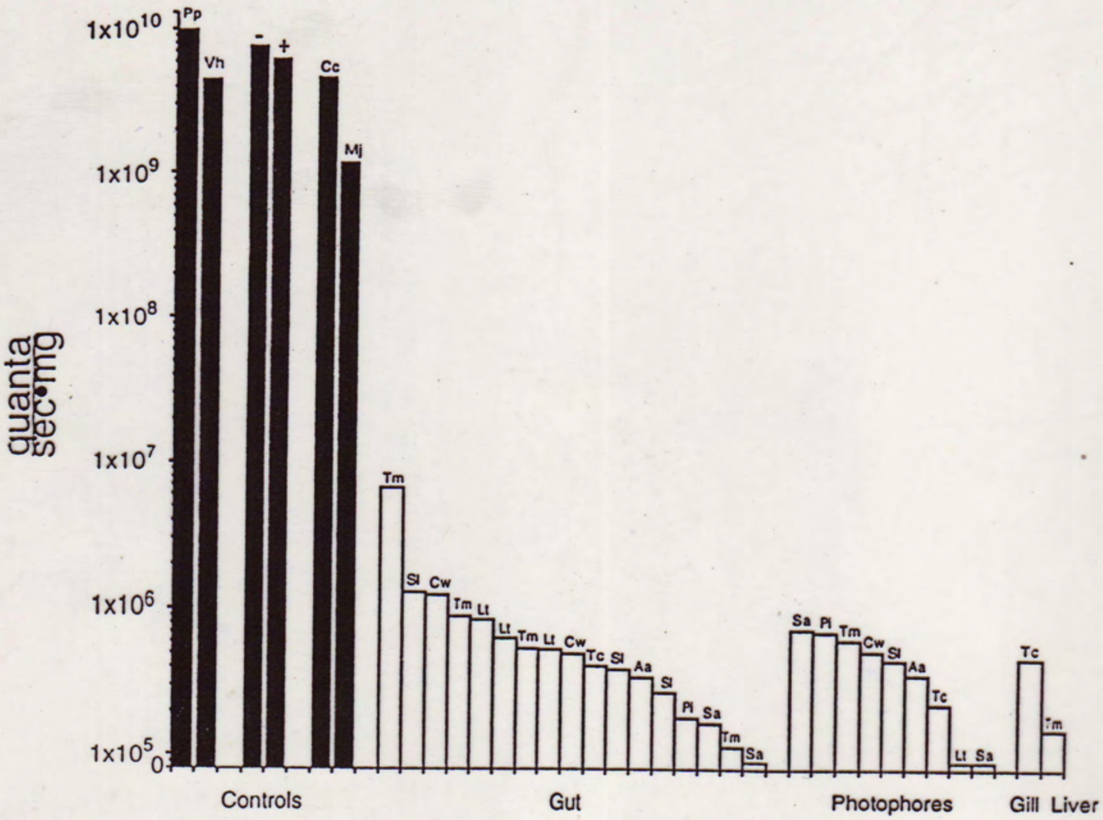


Fig. 2. Results of bacterial luciferase assays. Mean activity of each sample is plotted. Abbreviations (Table 1) identify sample sources. Multiple samples were available for some species. Solid bars, bacterial and symbiotic light organ controls; open bars, myctophid and stomiiform samples grouped according to tissue type. Pp, Vh, means of all bacterial controls; +, –, *V. harveyi* extract plus or minus photophore extract. The lowest activity samples (Sa gut, Lt and Sa photophores) had no detectable activity and are plotted at the level of the detection limit.

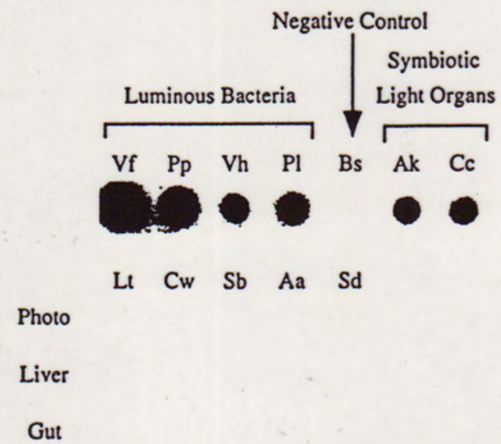
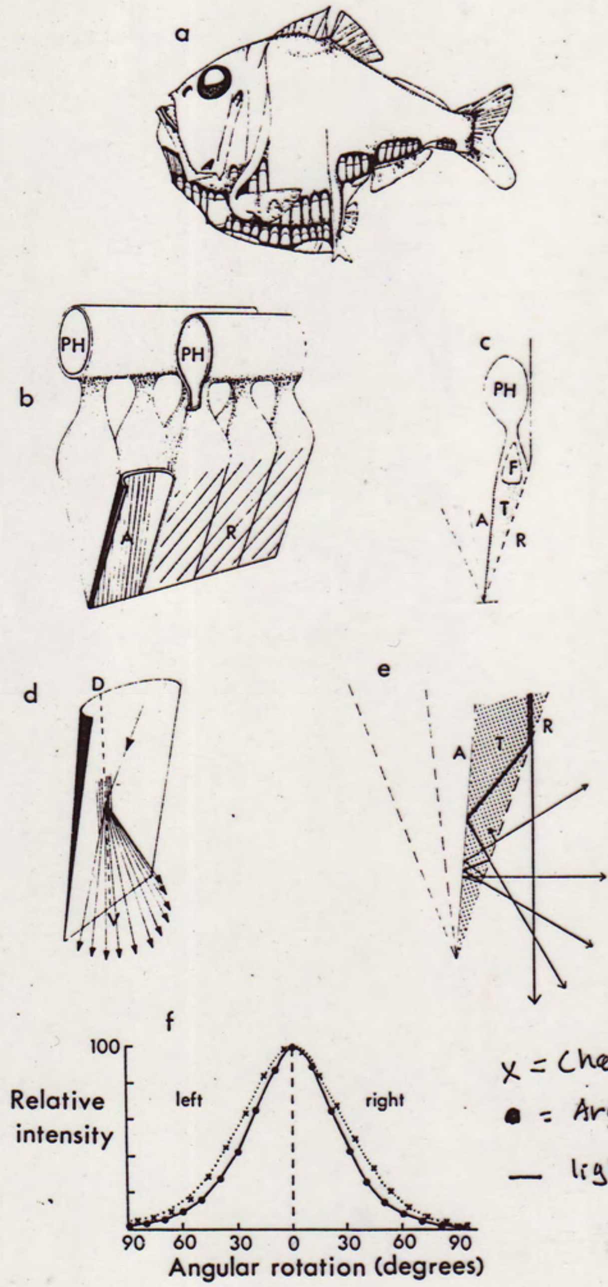


Fig. 3. Dot blot of DNA from positive and negative controls (top row) and tissues from myctophid and stomiiform fishes probed with a *lux* fragment analogous to pHU870. Abbreviations of species identification as in Table 2.



x = Chauliodus
● = Argyropelecus
— light in the sea