

PART ONE

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## Introduction and Historical Perspective

The medieval imagination, rioting in strange imps and hobgoblins, could hardly have invented anything more malevolent in appearance than the ceratioids or deep-sea anglerfishes, sometimes called black devils. Naturally enough, these black sea devils live in the kingdom of darkness, where they prowl about seeking whom they may devour. Many of them even carry a sort of torch, illumined with a phosphorescent glow, with which they lure their victims within reach of their devouring, traplike jaws.

GREGORY AND CONRAD,

"The Evolution of the Pediculate Fishes," 1936:193

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No place on earth can compete with the enormity of physical and biological constraints imposed on life in the deep oceanic midwaters. With temperatures near freezing, the absence of solar radiation, inconceivable pressures from the weight of water above, and biomass so low that meals are far and few between, it is almost inconceivable that animals could occupy this vast and forbidding habitat. Yet fishes are there in surprising profusion, having adapted to these extreme limitations in a host of bizarre and unpredictable ways. Few groups, however, are as prolific and spectacular as the deep-sea ceratioid anglerfishes.

Ceratioids are part of a much larger assemblage—an order of teleost fishes called the Lophiiformes—nearly all of which share a peculiar and unique mode of feeding characterized most strikingly by the structure of the first dorsal-fin spine (called the illicium), placed out on the tip of the snout and modified to serve as a luring apparatus to attract prey. The 18 families, 65 genera, and approximately 323 living species of the Lophiiformes are distributed among five suborders (Pietsch, 1984): the Lophioidei (Caruso, 1976, 1981, 1983, 1985, 1986; Caruso and Suttkus, 1979), Antennarioidei (Last et al., 1983, 2008; Pietsch and Grobecker, 1987), Chaunacoidei (Caruso, 1989a, 1989b), Ogcocephaloidei (Ochiai and Mitani, 1956; Bradbury, 1967, 1980, 1988, 1999; Endo and Shinohara, 1999), and deep-sea Ceratioidei (Fig. 1). The most phylogenetically derived of these suborders is the Ceratioidei, distributed throughout the world's oceans below a depth of 300 m (Pietsch, 1984; Pietsch and Orr, 2007). With 160 species, it constitutes by far the most species-rich vertebrate taxon within the bathypelagic zone and below (Fig. 2), containing more than twice as many families and genera and more than three times the number of species as the whalefishes—suborder Cetomimoidei—the next most species-rich deep-sea vertebrate taxon (see Paxton, 1998; Herring, 2002). At the same time, new species are being added to the suborder at a steady if not increasing rate.

Members of the group differ remarkably from their less-derived, bottom-living relatives by having an extreme sexual

dimorphism (shared by all contained taxa) and a unique mode of reproduction in which the males are dwarfed—those of some linophrynids, adults at 6–10 mm standard length, competing for the title of world's smallest mature vertebrates (see Winterbottom and Emery, 1981; Roberts, 1986; Weitzman and Vari, 1988; Kottelat and Vidthayanon, 1993; Watson and Walker, 2004; Pietsch, 2005b; Kottelat et al., 2006; Guinness World Records 2007:41)—and attach themselves (either temporarily or permanently) to the bodies of relatively gigantic females (Figs. 3, 4). In *Cerattias holboelli*, the Northern Giant Seadevil, where the most extreme examples are found, females may be more than 60 times the length and about a half-a-million times as heavy as the males (Bertelsen, 1951; Pietsch, 1976, 1986, 2005b; see also Guinness World Records, 2009). The males lack a luring apparatus, and those of most species are equipped with large well-developed eyes (Munk, 1964, 1966) and huge nostrils (Marshall, 1967a, 1967b), the latter apparently used for homing in on a female-emitted, species-specific chemical attractant (Bertelsen, 1951; Pietsch, 1976, 2005b; Munk, 1992). Normal jaw teeth of males are lost during metamorphosis but are replaced by a set of pincerlike denticles at the anterior tips of the jaws for grasping and holding fast to a prospective mate (Figs. 5, 6).

In some taxa, attachment is followed by fusion of epidermal and dermal tissues and, eventually, by an apparent connection of the circulatory systems so that the male becomes permanently dependent on the female for blood-transported nutrients, while the host female becomes a kind of self-fertilizing hermaphrodite (Regan, 1925a, 1925b, 1926; Parr, 1930; Regan and Trewavas, 1932; Bertelsen, 1951; Pietsch, 1975, 1976, 2005b; Munk and Bertelsen, 1983; Munk, 2000). Permanent attachment is usually accomplished by means of separate outgrowths from the snout and tip of the lower jaw of the male, both of which eventually fuse with the skin of the female. In some species, a papilla of female tissue protrudes into the mouth of the male, sometimes appearing to completely occlude the pharynx. The heads of some males become broadly

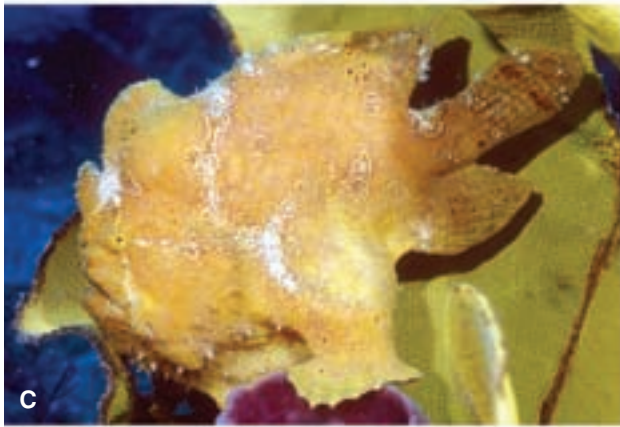
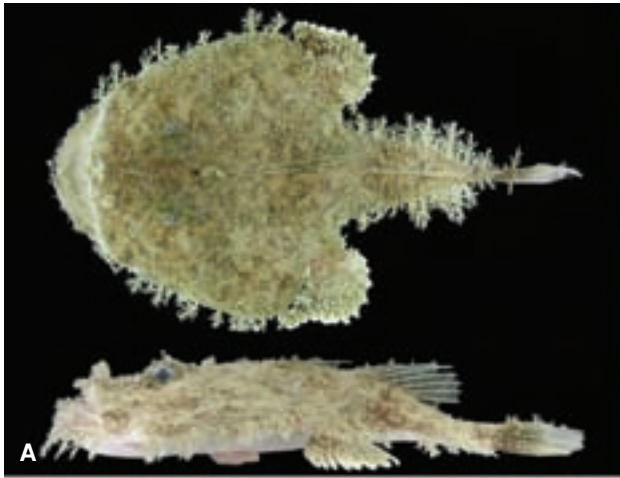
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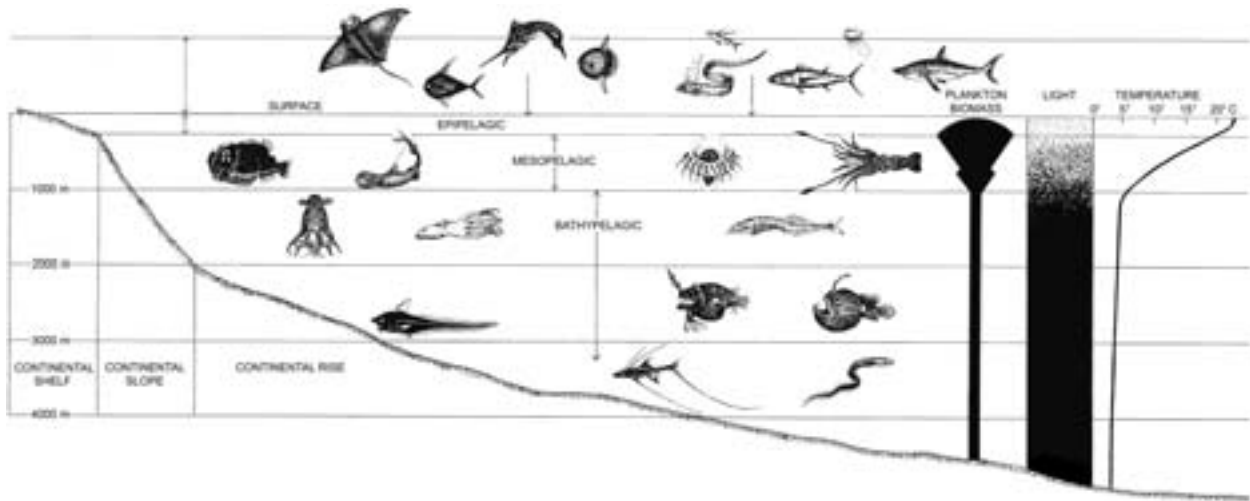


FIGURE 2. The ocean divided. For ease of discussion, oceanographers have divided the oceanic realm into a number of “zones” that are defined by both biological and physical-chemical parameters: the epipelagic zone extends from the surface to 200 m, a depth that corresponds on average to the margin of the continental slope, which in turn is approximately equivalent to the lower limit of photosynthesis, often called the euphotic zone; in terms of fishes, it provides habitat for many large, fast-swimming, predaceous forms like the tunas and mackerels, dolphin-fishes, billfishes, and ocean-going sharks; it also serves as a nursery ground for tons of eggs and larvae of deeper-living forms. The mesopelagic zone lies between 200 and 1000 m, this greater depth corresponding to the limit of penetration of solar radiation, often called the twilight zone or disphotic zone; it supports mostly silvery fishes with large eyes and light-producing structures called photophores; communication between individuals and species is primarily mediated by vision and biological light. The bathypelagic zone extends from 1000 to 4000 m, below the extent of solar radiation, often called the aphotic zone; it contains mostly black fishes with small or degenerate eyes, poorly developed musculature, and weakly ossified skeletons; communication is mostly by way of waterborne chemicals and a highly developed sense of smell. The abyssopelagic zone includes all the deepest parts of the ocean below 4000 m, providing habitat for things like hagfishes, certain squaloid sharks, deep-sea skates, deep-sea cods, eelpouts, snailfishes, rattails, and more; communication is largely through sound production and well-developed hearing abilities. At the right of the diagram are represented the change of biomass with depth, the penetration of sunlight, and a typical temperature profile of a warm ocean. While the term “pelagic” refers to everything that lies within the water column, benthopelagic describes all those phenomena and things that are closely associated with the bottom, regardless of depth, and benthic is reserved strictly for those things that spend all or nearly all their time resting on the bottom. Epipelagic animals (top row) from left to right: giant devil-ray (*Manta*), ocean bream (*Taractichthys*), spearfish (*Tetrapturus*), ocean sunfish (*Mola*), ribbon-fish (*Regalecus*), and above, flying-fish, long-fin tuna, Portuguese-man-of-war (*Physalia*), on surface, and great white shark (*Carcharodon*). Mesopelagic animals, left to right: hatchet-fish (*Agyroplecus*), viperfish (*Chauliodus*), coronate jellyfish (*Atolla*), squid (*Histioteuthis*). Bathypelagic animals, left to right: *Vampyroteuthis*, midwater octopod (*Amphitretus*) both of which live also at mesopelagic levels, *Cyclothone*, and immediately below, two female ceratioid anglerfishes (*Linophryne* and *Melanocetus*). Bottom-dwelling fishes, left to right: Rat-tail (*Nezumia*), a benthopelagic form, tripodfish (*Bathypterois*), a benthic form, and a deep-sea eel (*Synphobranchus*), a benthopelagic form. Modified after Marshall (1974).

fused to the skin of the female, extending from the tip of the lower jaw to the rear of the skull, appearing as if embedded or absorbed by their mate, while in others, the male is carried at the tip of an elongate, cylindrical stalk of female tissue. Increasing considerably in size once fused, their volume becoming much greater than free-living males of the same species, and being otherwise completely unable to acquire nutrients on their own, the males are considered to be parasites. They apparently remain alive and reproductively functional as long as the female lives, participating in repeated spawning events. A single male per female appears to be the rule in some taxa, but in others multiple attachments are relatively common, with as many as eight coupled to a single host (Saruwatari et al., 2001). Since its discovery

more than 80 years ago (Saemundsson, 1922; Regan, 1925a, 1925b), the story of sexual parasitism in ceratioid anglerfishes has become a part of common ichthyological knowledge. However, the known facts concerning this remarkable reproductive mode have never been thoroughly or satisfactorily analyzed, despite the work of Bertelsen (1951) and more recently of Munk and Bertelsen (1983), Munk (2000), and Pietsch (2005b). The physiological mechanisms (endocrinological and immunological) that allow for sexual parasitism, which could be of significant biomedical importance, have never been explored.

Ceratioid anglerfishes differ further from their less-derived bottom-dwelling relatives in having a bacterial light-organ that serves as bait to attract prey (for the possibility of bioluminescence

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FIGURE 1. The five suborders of anglerfishes that together form the teleost order Lophiiformes: (A) Lophioidei, containing the goosefishes or monkfishes, a single family, four genera, and 25 living species of shallow to deepwater, dorsoventrally flattened forms (represented here by *Lophiodon reticulatus*, 157 mm SL, UF 158902, dorsal and lateral views, photo by J.H. Caruso); (B-E) Antennarioidei, the frogfishes and handfishes, four families, 15 genera, and about 54 species of laterally compressed, shallow to moderately deepwater, benthic forms (represented by *Antennarius commersoni*, 111 mm SL, UW 20983, photo by D. B. Grobecker; *Antennarius commersoni*, about 150 mm SL, specimen not retained, photo by F. Schneidewind; *Antennarius striatus*, 150 mm SL, specimen not retained, photo by F. Schneidewind; *Brachionichthys politus*, specimen not retained, photo by R. Kuitert); (F) Chaunacoidei, the gapers, coffinfishes, or sea toads, a single family, at least two genera, and as many as 14 species of globose, deepwater benthic forms (*Chaunax umbrinus*, 305 mm SL, BPBM 17344, photo by J.E. Randall); (G) Ogcocephaloidei, the batfishes, a single family of 10 genera and about 68 species of dorsoventrally flattened, deepwater benthic forms (*Haliutaea retifera*, 102 mm SL, BPBM uncataloged, dorsal view, photo by J.E. Randall); and (H) Ceratioidei, the seadevils, containing 11 families, 35 genera, and 160 currently recognized species of globose to elongate, mesopelagic, bathypelagic, and abyssal-benthic forms (*Diceratias trilobus*, 86 mm SL, AMS L31144-004, photo by T.W. Pietsch).

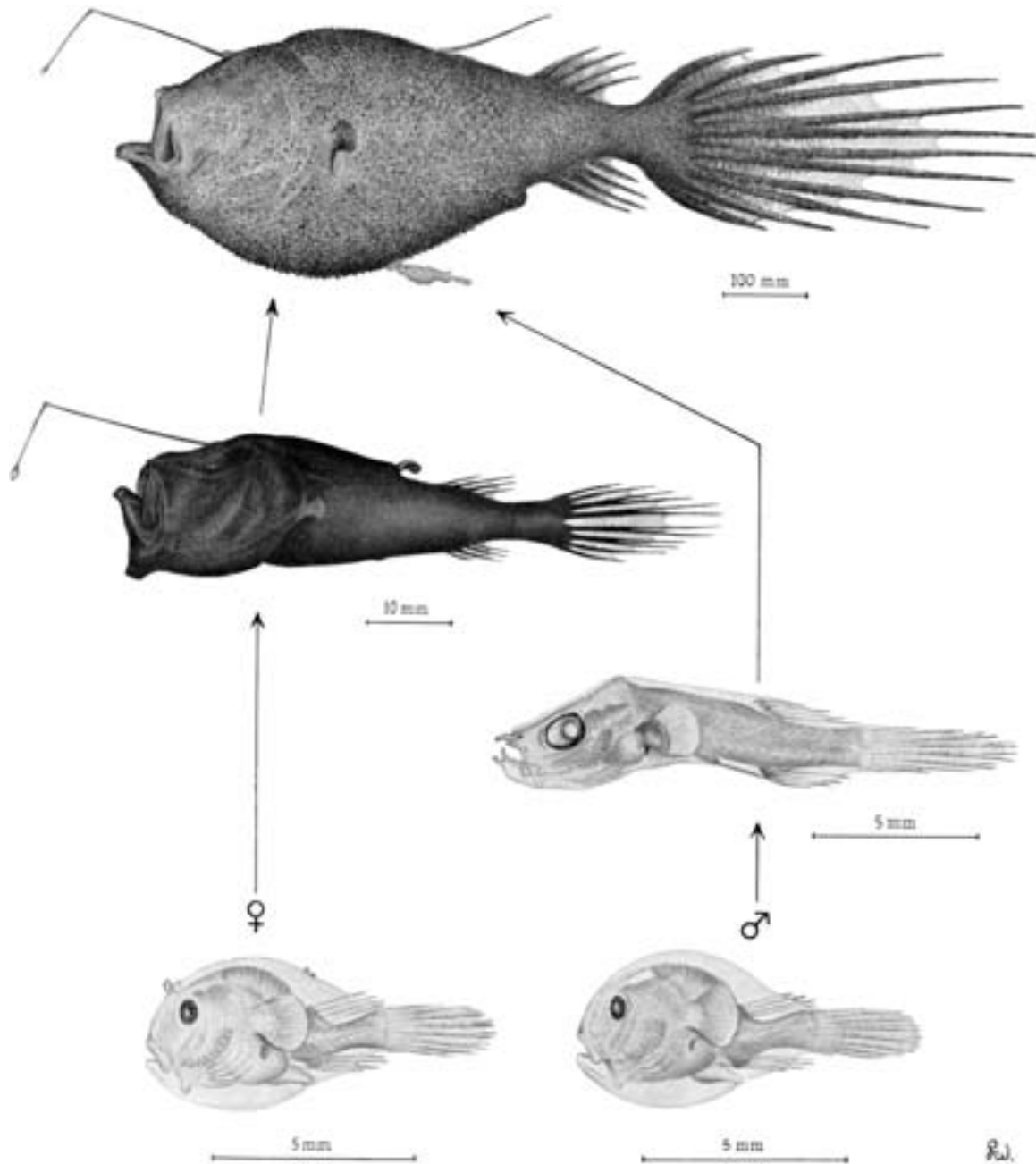


FIGURE 3. The life history of *Ceratias holboelli* Krøyer, the Northern Giant Seadevil: female and male larvae, shown at the bottom of the diagram, exist in the plankton of the epipelagic zone in roughly equal numbers; rudiments of the developing illicium are present even in the tiniest females, thus gender can be easily determined immediately after the eggs hatch; during metamorphosis the female rapidly increases in size, the illicium elongates, and the skin becomes darkly pigmented, while the eyes become reduced and eventually covered over with black skin; the male develops pincherlike denticular teeth on the tip of the snout and chin, and the eyes increase in relative size as he begins his search for a conspecific female; once found, the male attaches to the female, and the tissues of the two eventually fuse, resulting in permanent parasitic conjugation. Drawings by Poul H. Winther; after Bertelsen (1951).

in batfishes, see Crane, 1968). Placed out on the tip of the illicium, the bait, or “esca” as it is technically called, is species-specific; that is, in external appearance it differs without exception in all members of the suborder. Parr (1927) was the first to recognize the diagnostic value of the external morphology of escae in ceratioids, pointing out the need for a closer examination of individual variation in the structure of this organ. Regan and Trewavas (1932:3-4) agreed, employing small differences in esca morphology to introduce 45 oneirodid species as new to science (in the following quote, for “illicium,” read “esca”):

It now appears that the Oneirodidae may attain the form of the adult when quite small, and that in this family, specimens only 15 to 20 mm long may show a definite and characteristic structure of the illicium. Although we cannot be sure that specimens that differ only in slight details of the illicium are specifically distinct, and we do not like basing new species on single specimens 15 mm in total length, we consider that to give specific names freely is probably the best way to describe the material now available.

Since that time, differences in the number, shape, and size of esca appendages and filaments, as well as variation in

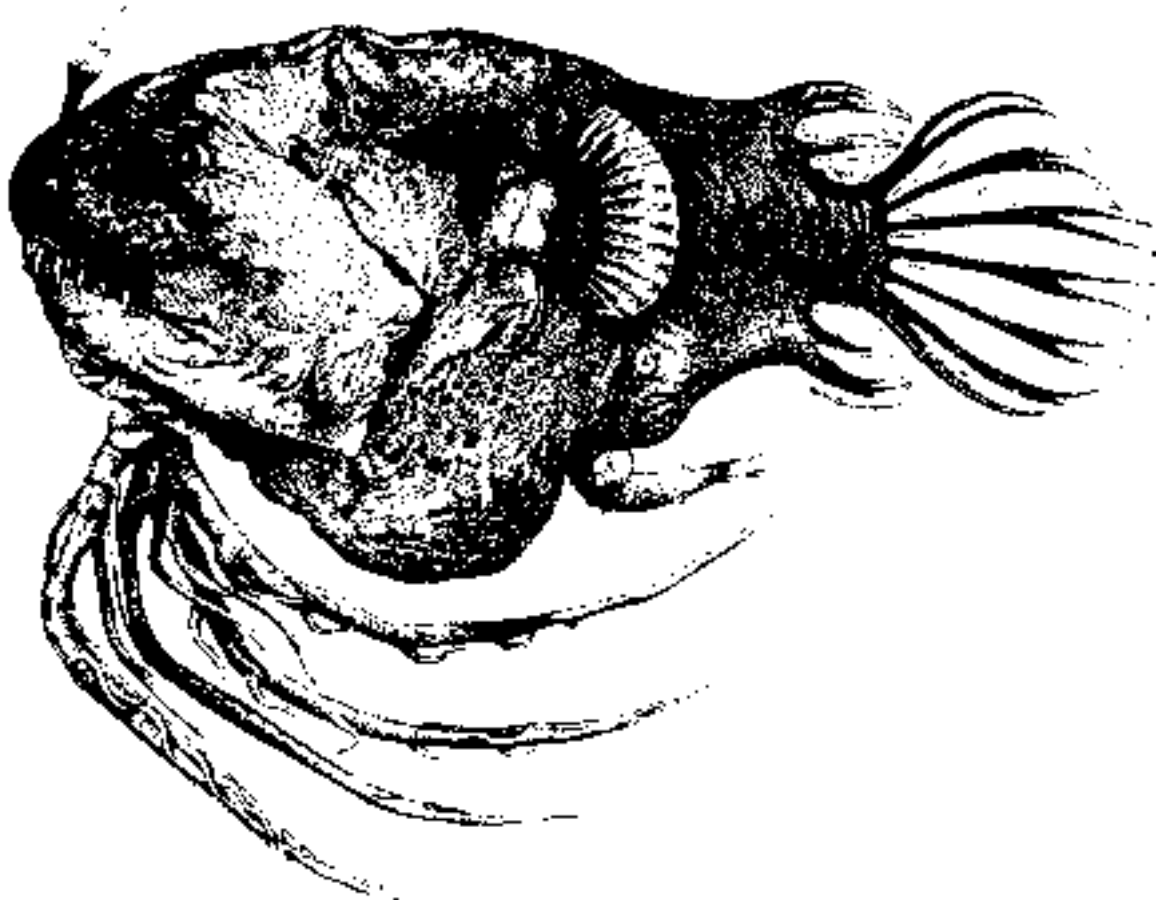


FIGURE 4. *Linophryne brevibarbata*, 100-mm SL female, with an 18.5-mm SL parasitic male, BMNH 1995.1.18.4, a North Atlantic species known from only six specimens. Drawing by Elisabeth Beyerholm; after Bertelsen (1980a).



FIGURE 5. Head of a free-living male of the *Linophryne arborifera* group, 18.5 mm SL, BMNH 2004.7.5.1, showing the denticular teeth and extremely well-developed eyes and nostrils. Drawing by Robert Nielsen; after Bertelsen (1980a).

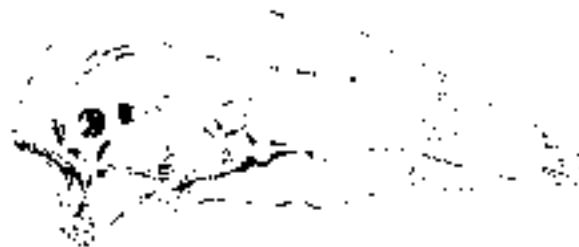


FIGURE 6. A free-living male of *Haplophryne mollis*, 13 mm SL, ZMUC (specimen sacrificed for histological study), with its mouth agape, indicating the effectiveness of the jaw apparatus in attaching to a female. Drawing by R. Nielsen; after Munk and Bertelsen (1983).

external esca pigment patterns, have been, for the most part, the sole basis on which new species have been described (e.g., see Pietsch, 1974a; Bertelsen et al., 1981; Bertelsen and Krefft, 1988).

The internal structure of ceratioid escae is infinitely more complex, involving a confusing array of bacteria-filled vesicles, light-absorbing pigment layers, reflecting tissues, tubular light-guiding structures, nerves, blood vessels, and smooth muscle fibers (Munk and Bertelsen, 1980; Munk, 1988, 1998, 1999; Herring and Munk, 1994; Munk and Herring, 1996; Munk et al., 1998). There is some evidence also that ceratioid escae contain pheromone-producing secretory glands that function to attract a conspecific male (Munk, 1992), but the

true nature and adaptive significance of these structures and most of the other internal parts of escae are unknown.

In addition to the esca, all 22 currently recognized species of the ceratioid genus *Linophryne* (family Linophrynidae) bear an elaborate bioluminescent chin barbel, the light of which does not originate from symbiotic luminescent bacteria, but rather from a complex array of intrinsic, intracellular, paracrystalline photogenic granules; the bacteria-filled esca is ectodermal in origin, whereas the barbel light organ appears to be derived from the mesoderm (Hansen and Herring, 1977). This remarkable dual system, involving two entirely separate mechanisms of light production, is unique among animals.



FIGURE 7. Henrik Nikolai Krøyer (1799–1870), a painting by his stepson, the well-known Norwegian-Danish artist Peder Severin Krøyer (1851–1909), dated 1872. Courtesy of Peter Rask Møller, Jørgen Nielsen, and the Zoological Museum, University of Copenhagen.

In summary, ceratioid anglerfishes are among the most intriguing of all animals, possessing a host of spectacular morphological, behavioral, and physiological innovations found nowhere else. The suborder is taxonomically diverse: with 160 currently recognized species (and many more certain to be discovered in the future), it forms a major contribution to the biodiversity of the deep sea. It is exceedingly widespread geographically, occurring in deep waters of all major oceans and seas of the world, from high Arctic latitudes to the Southern Ocean; while some species appear to be almost cosmopolitan in distribution, many others have surprisingly small, restricted vertical and horizontal ranges. Their relative abundance, high species diversity, and trophic position as the top primary carnivores in meso- and bathypelagic communities make them important ecologically. Their unique mode of reproduction has significant biomedical implications to the fields of endocrinology and immunology. Yet, despite these many aspects of biological interest and importance, as well as a large amount of revisionary work published in the 1970s and early 1980s—including repeated attempts to resolve phylogenetic relationships—ceratioid anglerfishes have remained poorly known. Well short of providing all the answers, it is hoped that this monograph will have established a firm basis for future research and discovery.

### Historical Perspective

In 1833, following a severe storm, a strange and unknown fish was washed ashore near Godthaab, southwest Greenland. It was remarkable for its nearly spherical head and body, large mouth, the absence of pelvic fins, thick black skin sparsely set with large spine-bearing bony plates, restricted gill openings,

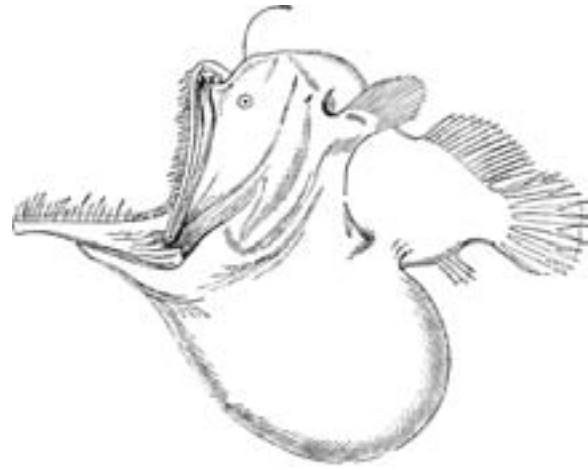


FIGURE 8. Albert Günther's holotype of *Melanocetus johnsonii*, female, 64 mm SL, BMNH 1864.7.18.6, brought to London from Madeira by James Yates Johnson (c. 1820–1900) and described by Günther in 1864: "It must be extremely rare, as the specimen entrusted to me by Mr. Johnson for description, and presented by him to the British Museum, is the only one which has ever come to the knowledge of naturalists." After Günther (1880).

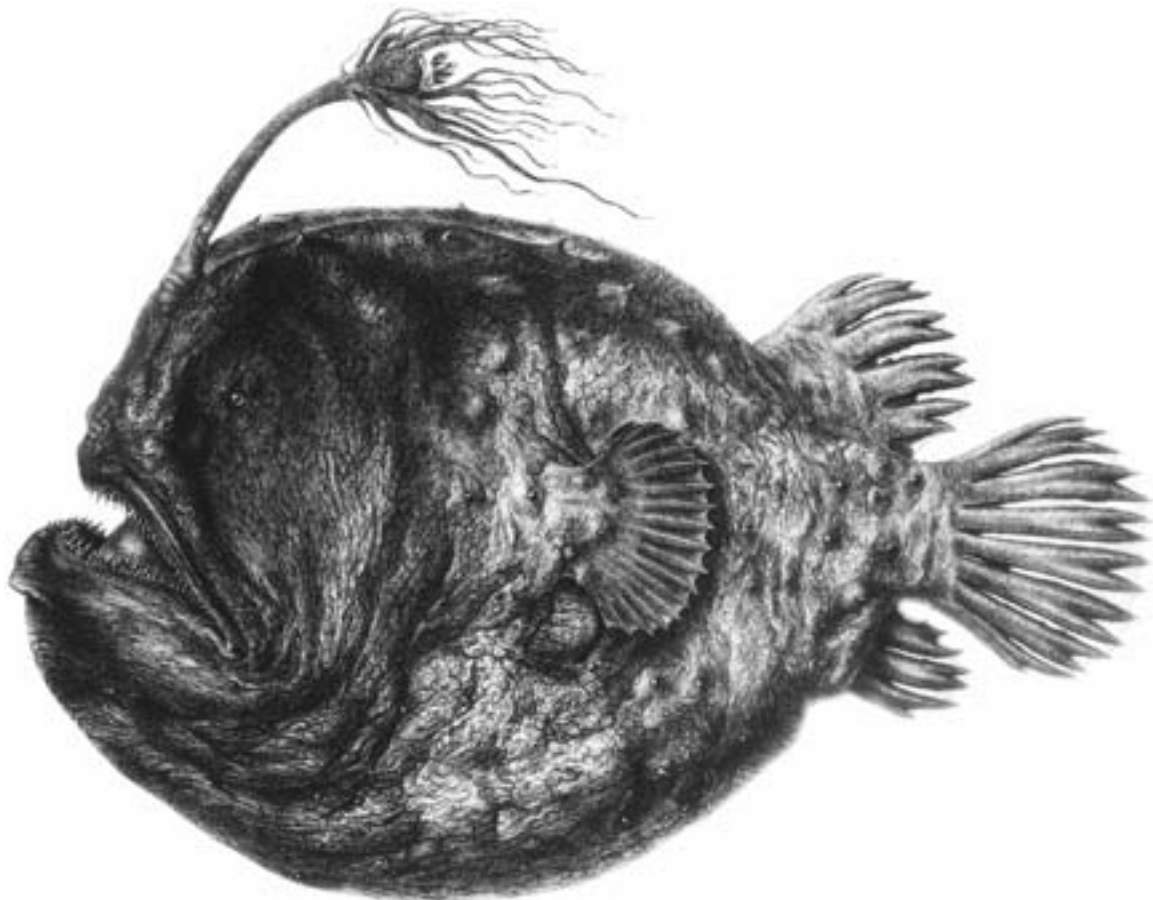
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and a conspicuous flexible appendage arising from a deep longitudinal groove on the forehead, terminating in a series of elongate filaments (Waterman, 1939a). The specimen was badly damaged by birds and decay, but fortunately it was preserved and given to Captain-Lieutenant Carl Peter Holbøll (1795–1856), who in turn sent it to Johannes Christopher Hagemann Reinhardt (1776–1845), then professor of zoology at the University of Copenhagen. In 1837, Reinhardt described the specimen and named it *Himantolophus groenlandicus*, the first representative of the suborder Ceratioidei known to science. Reinhardt noted its similarities to *Lophius* and *Antennarius* in body shape, in position and structure of the gill openings, and in the development of the large anterior cephalic fin spine, but the differences from these well-known shallow-water genera, especially the absence of pelvic fins, left him in doubt about its relationships (Bertelsen, 1951). In the end, however, he concluded that his new species was most probably related to those fishes that comprise the teleost order Pediculati (Regan, 1912).

The same Captain Holbøll who sent the first known specimen of *Himantolophus groenlandicus* to Reinhardt later obtained from deep waters off Greenland two additional ceratioids (originally called *barbugede Tudsefiske* or "bare-bellied toadfishes" by the Danes, because pelvic fins are absent in metamorphosed specimens of all known representatives). One of these specimens was described in 1845 by Danish ichthyologist and carcinologist Henrik Nikolai Krøyer (Fig. 7) as *Cerantias holboelli*. The other, sent by Holbøll to physiology and anatomy professor Daniel Frederic Eschricht (1798–1863), was eventually accessioned into the collections of the University of Copenhagen, where it remained unnoticed for the next 25 years.

In the meantime, Albert Carl Ludwig Gotthilf Günther (1830–1914), keeper of zoology at the British Museum in London, received a very different looking ceratioid from James Yates Johnson (c. 1820–1900) who brought it back from Madeira in 1864: "A fish which proves to be the type of a new genus, not only on account of its extraordinary form, but also on account of the absence of pelvic fins. In the latter respect it agrees with *Cerantias* from the coast of Greenland, from





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FIGURE 9. Christian Frederik Lütken's holotype of *Himantolophus reinhardti*, female, 328 mm SL, ZMUC 66, a name now in the synonymy of *Himantolophus groenlandicus*; by any standard, one of the most accurate and detailed illustrations of a ceratioid ever published. After Lütken (1878).

which, however, it differs in its dentition" (Günther, 1864:301). This new form, remarkable for its large pendulous belly—which when opened was found to contain, "rolled up spirally into a ball, a Scopeline fish" nearly twice the length of the angler—was described by Günther in that same year and named *Melanocetus johnsonii* in honor of its collector (Fig. 8).

Some time later, back in Denmark, yet another Danish professor, Christian Frederik Lütken (1827–1901), came across Eschricht's long forgotten Greenland specimen in the collections of the University of Copenhagen. Recognizing it as distinct from the three previously known genera, but most similar to Günther's *Melanocetus* in lacking skin spines, among other similarities, he described it in 1871 (1872 in English translation) under the name *Oneirodes eschrichtii*: "That the Greenland form is specifically distinct from the deep-sea Lophioid from Madeira [*Melanocetus*], which has been so often mentioned, is seen at first glance. Their differences, notwithstanding their resemblance in many essential features, are very sharply marked; nay, I consider that it will even be admitted that they are great enough for the establishment of a generic distinction (Lütken, 1872:330–331)."

In many ways, Lütken's 1871 paper and another published in 1878—in which he described *Himantolophus reinhardti* based on a second known specimen of the genus, also from West Greenland—represent "remarkable pioneer work," not only on the Himantolophidae, but on ceratioids in general (Bertelsen and Krefft, 1988:10). In addition to providing exact and

extremely detailed descriptions and illustrations of the specimens (Figs. 9, 10), Lütken was the first to recognize that the four ceratioid genera known at that time, *Himantolophus*, *Cerantias*, *Melanocetus*, and *Oneirodes*, together represent a discrete taxon (which he called *Lophioidea apoda* or *les Céратиades*) within the then-recognized anglerfish order Pediculati: "Between all of these [genera] there is the nearest affinity; and they seem to form a very natural little group of deep-sea Lophioids, of weak vision and destitute of pelvic fins, within the great family of the Halibatrachi" (Lütken, 1871:70, 1872:340; see also Lütken, 1878b:342, 343). In this he preceded Theodore Nicholas Gill (1837–1914), who in 1873 included *Himantolophus*, *Cerantias*, and *Oneirodes* in the family Ceratiidae, the latter family-group name dating to Gill (1861). Although Reinhardt (1837), in describing the illicium of *Himantolophus*, certainly implied its use as a lure, Lütken (1878a) was the first to specifically state the probability that the first dorsal-fin spine (as in other lophiiform fishes) is used to attract prey (p. 325) and that the terminal bait or esca is bioluminescent (p. 313; but see also Willemoes-Suhm, 1876, and the somewhat later account of Collett, 1886:138, 142). He also provided the first osteological description of a ceratioid (Fig. 11), as well as a discussion of the importance of esca morphology, including the position, number, and shape of the various esca appendages, as characters that can be used to differentiate taxa (1878:318; Fig. 10). Finally, he was the first to describe and illustrate a larval ceratioid, correctly referring it to *Himantolophus* (1878a:321–324; Fig. 10).

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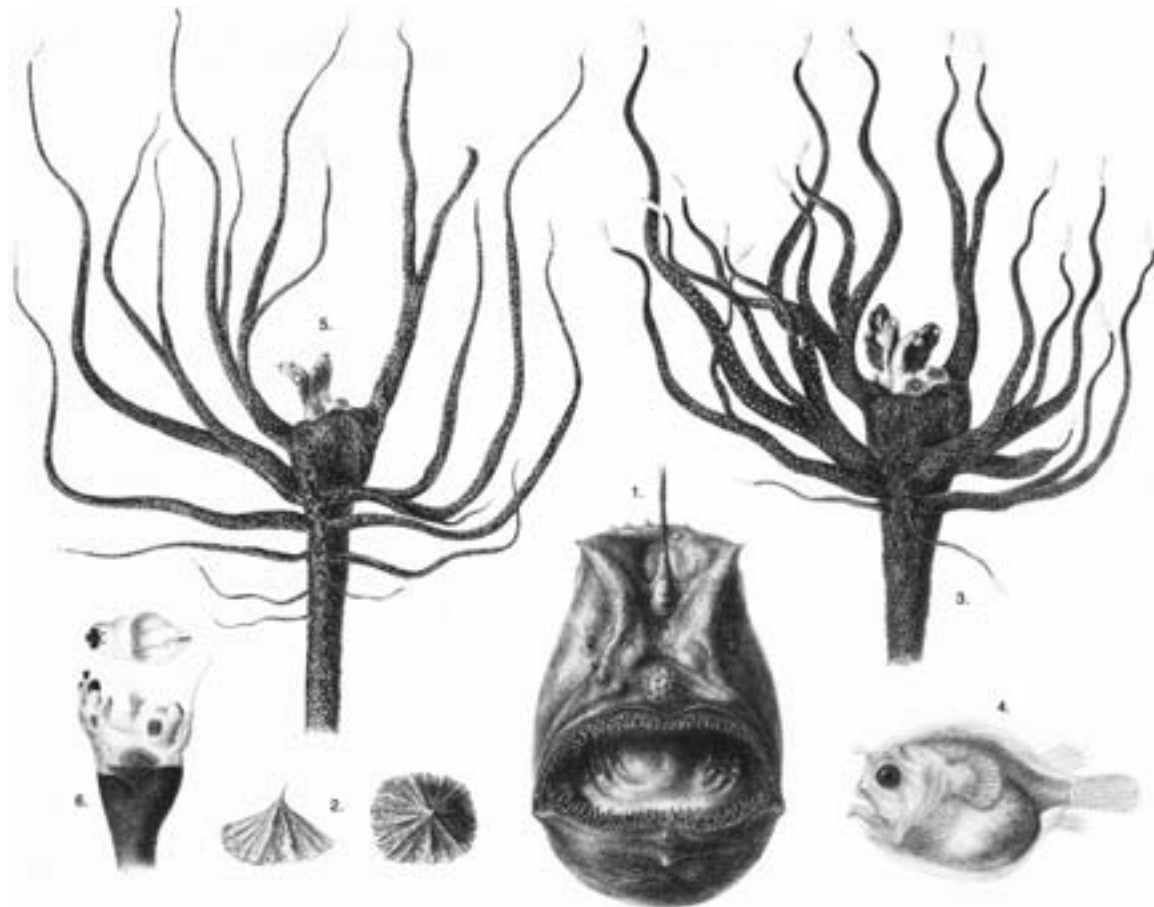


FIGURE 10. Illustrations taken from Lütken's publication on "Dybhavs-Tudsefiske" (deep-sea toadfishes): **(1)** Anterior view of the holotype of *Himantolophus reinhardtii*, female, 328 mm SL, ZMUC 66; **(2)** lateral and dorsal views of large conical spines from the skin of *Himantolophus reinhardtii*; **(3)** esca of the holotype of *Himantolophus reinhardtii*; **(4)** a larval female of *Himantolophus* sp., about 18 mm SL; **(5)** esca of the holotype of *Himantolophus groenlandicus*, ZMUC 65; **(6)** lateral and dorsal views of the esca of the holotype of *Oneirodes eschrichtii*, 153 mm SL, ZMUC 64, described by Lütken in 1871. After Lütken (1878).

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or b?

Following these initial discoveries, a few additional species were described based on single specimens caught incidentally in trawls or, more often, found dead on shore or floating on the surface. Notable among the latter are *Himantolophus appellii*, described in 1878 by Frank Edward Clarke (1849–1899) from a single specimen found stranded on a New Zealand beach (Fig. 12); and *Linophryne lucifer*, described in 1886 by Robert Collett (1842–1913) from a specimen found floating alive on the surface off Madeira apparently, incapacitated by ingestion of a large fish (Fig. 13). But it was not until the great oceanographic expeditions of the late nineteenth and early twentieth centuries that ceratioids become known in any reasonable numbers. The circumnavigation of the HMS *Challenger* (1872–1876) brought back half a dozen specimens, by far the largest single collection to date and the first specimens to be collected in their natural environment. From this material, Sir John Murray (1841–1914), an eminent deep-sea biologist and one of the founders of modern oceanography (Mills, 1989), described *Ceratias uranoscopus* in Charles Wyville Thomson's (1830–1882) *Voyage of the Challenger*, first published in 1877. Likewise, from this same collection, Günther, in his "Challenger" report on the deep-sea fishes of 1887, described *Melanocetus murrayi* and *Diceratias bispinosus*, recognizing overall eight genera and eleven ceratioid species based on the thirteen specimens then known in collections around the world.

Material collected during the numerous scientific cruises of the U.S. Fish Commission Steamer *Albatross* (from 1883 to 1920) provided considerably larger collections (Hobart, 1999), from which Gill described *Cryptopsaras couesii* in 1883; George Brown Goode (1851–1896) and Tarleton Hoffman Bean (1846–1916), *Caulophryne jordani* in 1896; Samuel Walton Garman (1843–1927), *Dolopichthys allector* in 1899; Hugh McCormick Smith (1865–1941) and Lewis Radcliffe (1880–1950), *Dermatias platynogaster* and *Thaumatichthys pagidostomus*, both in 1912; and Charles Henry Gilbert (1859–1928), *Oneirodes acanthias* in 1915.

Samuel Garman's (1899) description of *Dolopichthys allector* that appeared in his "Report on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U. S. Fish Commission steamer *Albatross*" is remarkable for its accuracy, detail, and beautiful illustrations (Figs. 14–16). With only a single small specimen available to him, Garman, through a series of careful dissections, was able to describe not only the complete skeleton, but the musculature as well, including that of the head, body, fins, and even the illicial apparatus. More surprising are his descriptions and figures of the gills and the viscera, the latter providing the earliest depiction of the internal organs of an anglerfish. In all of this he was well ahead of his contemporaries, and for completeness and accuracy he has rarely been eclipsed since.

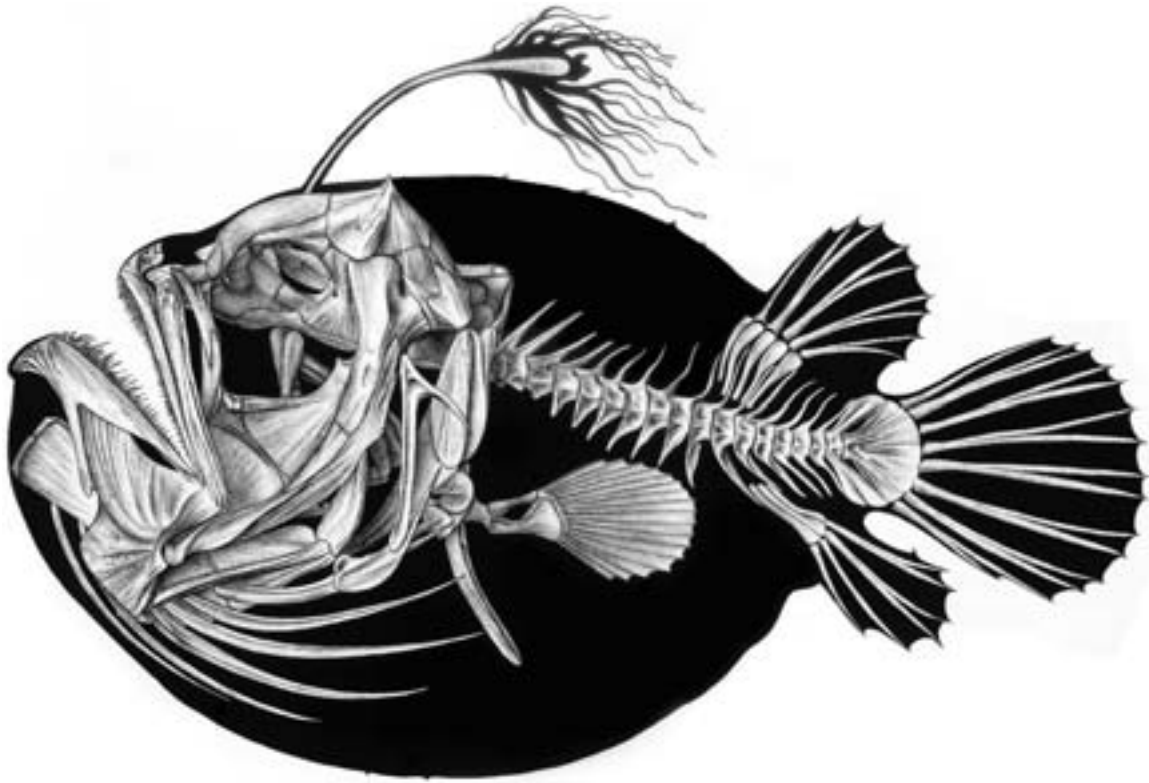
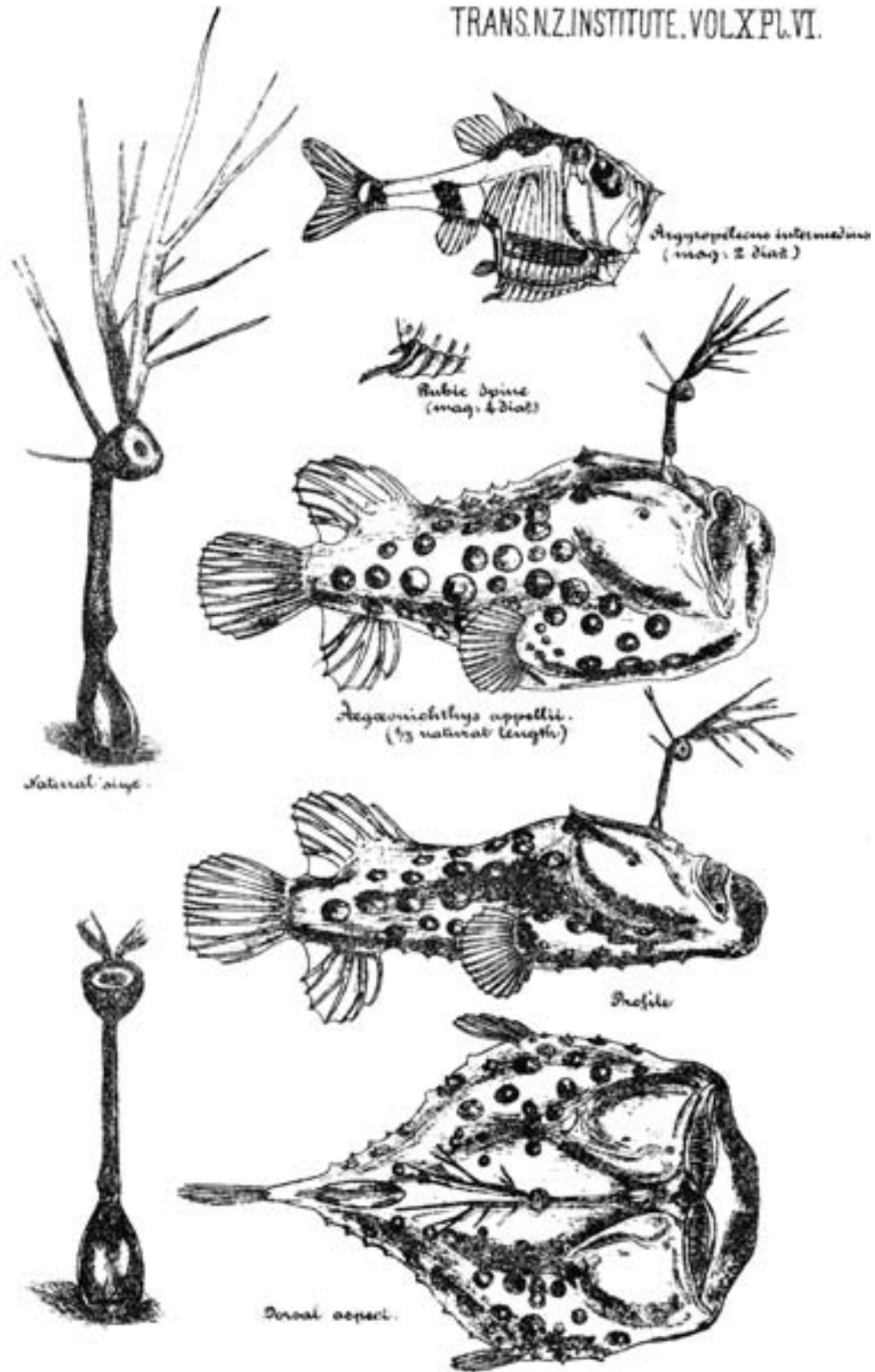


FIGURE 11. The skeleton of *Himantolophus groenlandicus*, female, 148 mm SL. After Lütken (1887).

August Bernhard Brauer (1863–1917), one-time director of the Zoological Museum of the Humboldt University of Berlin, in his 1902 report on the fishes collected during the German *Valdivia* Expedition of 1898–1899, described four new ceratioid species, recognizing overall a total of 23 species in three families, the Ceratiidae, Gigantactinidae, and Aceratiidae. One of these families, the Aceratiidae, was introduced by Brauer (1902) to contain some small anglerlike fishes that were similar to ceratiids and gigantactinids in the absence of pelvic fins and having restricted gill openings, but differed in lacking a cephalic luring apparatus. A decade later, Charles Tate Regan (1878–1943) of the British Museum of Natural History (Fig. 17), in revising the classification of anglerfishes based in part on an osteological examination, placed all those taxa lacking pelvic fins in a separate suborder, the Ceratioidei, which he divided into six families, including Brauer's Aceratiidae (Regan, 1912). Neither Brauer (1902) nor Regan (1912) was aware at the time that these little ceratioids without lures were actually the males of species based at that time only on females. The discovery of the remarkable sexual dimorphism that characterizes all ceratioids would have to wait until May 1924, when Regan realized that a small fish attached to the side of a large female *Cerantias holboelli* was in fact a "dwarfed parasitic male" (Regan, 1925a:41, 1925b:386; for more on dwarfed males and the history of the discovery of sexual parasitism, see Reproduction and Early Life History, Chapter 8).

By far the greatest contribution to our knowledge of the Ceratioidei up until that time came from the Danish oceanographic expeditions aboard the Royal Danish Research Ship *Dana* under the direction of Johannes Schmidt (1877–1933). Prior to these efforts, there were only about 100 known specimens, distributed among 16 genera and 24 species—including the 40 or so specimens collected during the *Michael Sars* North

Atlantic Deep-Sea Expedition of 1910, which were not described until 1944 by Einar Koefoed (but see John Murray and Johan Hjort, 1912; and Regan, 1926:3). However, the 1920–1922 *Dana* Expedition to the North Atlantic, Caribbean Sea, and Gulf of Panama alone took 217 specimens (excluding larvae). In reporting on this material, Regan (1925c, 1926) recognized 39 species, 27 of which were described as new, more than doubling the number of known species. The 1928–1930 Danish "Oceanographic Expedition Round the World," again under the leadership of Schmidt and funded this time by the Carlsberg Foundation, brought back 172 specimens, from which Regan, in coauthorship with Ethelwynn Trewavas (1900–1993), described 79 new species, once again more than doubling the number of recognized forms (Regan and Trewavas, 1932). These descriptions based on the *Dana* collections—in addition to those published by Albert Eide Parr (1927, 1930, 1934), William Beebe (1926, 1932), Nikolai Andreevich Borodin (1930a, 1930b), Viktor Pietschmann (1926), John Roxbrough Norman (1930), Leonard Peter Schultz (1934), Alan Fraser-Brunner (1935), Gérard Belloc (1938), Wilbert McLeod Chapman (1939), Talbot Howe Waterman (1939b), Sadahiko Imai (1941), and Beebe and Jocelyn Crane (1947)—greatly increased the known ceratioid biodiversity, so that by the time of Erik Bertelsen's (1951) worldwide revision of the suborder, the number of described species had risen to 194. A good number of these, however, have since fallen into synonymy; for example, of the 106 species described by Regan, either alone or in coauthorship with Trewavas, only 41 are recognized today; of the 17 described by Parr, only 4 are still recognized; and of the 20 described by Beebe, alone or in coauthorship with Crane, only 6 are still recognized today. Despite this high attrition, however, new ceratioids continue to be discovered.



*F. E. Clarke del* To illustrate paper by *F. E. Clarke*.

FIGURE 12. Frank Edward Clarke's illustrations of the holotype of *Aegoonichthys appellii*, female, 287 mm SL (specimen not retained), now known as *Himantolophus appellii*: "The fish forms a new genus in the family of Pediculati and is truly 'a king among kings' in a class of fishes containing some of the most grotesque forms in nature. After Clarke (1878).

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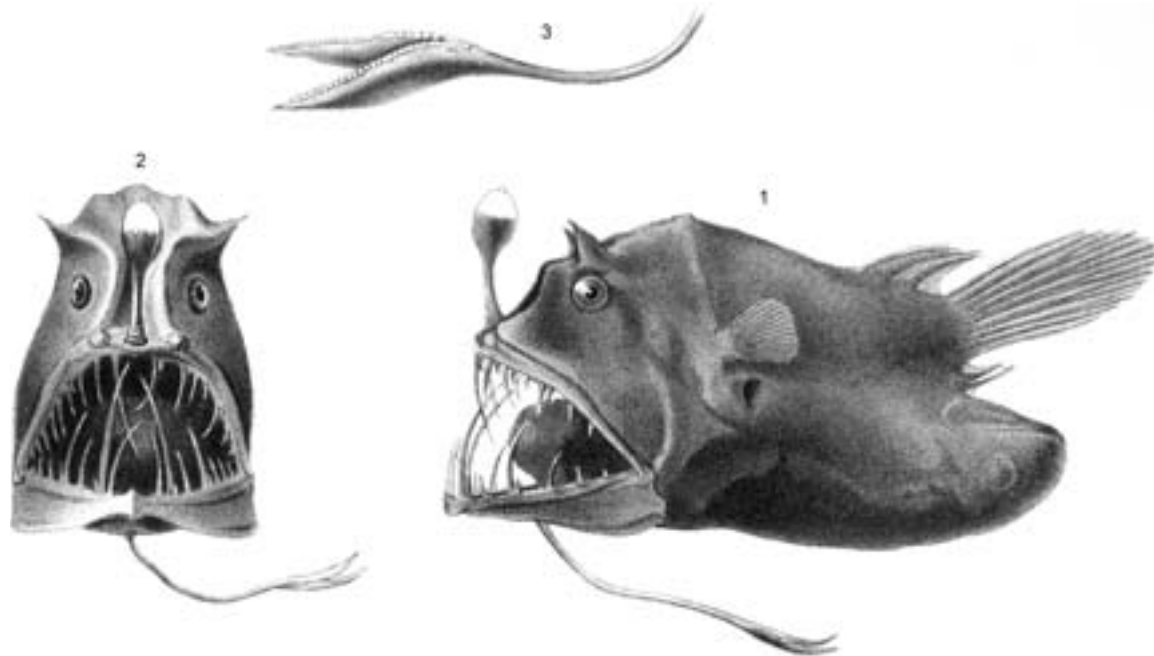


FIGURE 13. The holotype of *Linophryne lucifer*, female, 31.5 mm SL, ZMUO J.5560, discovered off the coast of Madeira by Captain P. Andresen, while on a voyage to the West Indies: "He was capturing turtle in his boat; there was a heavy swell, but the water was smooth. After a time he caught sight of this little black fish, which lay on the surface quite alive, but almost motionless, which was not surprising when it was discovered that it had just swallowed a fish longer than itself. It did not lie on its side, but was apparently unable to swim away. By getting the bailer under it, he lifted it out with ease, and in order to keep it fresh he gave up his search for turtle and rowed back to the ship, where it was placed in spirit for preservation." After Collett (1886).

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From an early date, it was believed that ceratioids were "degenerate" relatives of shallow-water, inshore anglerfishes, living much like *Lophius*, but at great depths in the open ocean, luring prey with their highly modified first dorsal-fin spine, while lying on soft muddy bottoms: "The Bathybial Sea-devils . . . are degraded forms of *Lophius*; they descend to the greatest depths of the oceans. Their bones are of an extremely light and thin texture, and frequently other parts of their organization, their integuments, muscles, and intestines, are equally loose in texture when the specimens are brought to the surface. In their habits they probably do not differ in degree from their surface representatives" (Günther, 1887:50).

When Reinhardt (1837) described the "frontal appendage" (illicium and esca) of *Himantolophus groenlandicus* as being the same as, but more highly developed than, that of *Lophius* and *Antennarius* (see Pietsch and Grobecker, 1987), he surely meant to imply its use as a lure to attract prey (Waterman, 1939a). Lütken (1871:62, 1872:334), however, as mentioned above, was the first to state this directly. In describing the bait at the tip of the first dorsal-fin spine of *Oneirodes eschrichtii*, he commented further on its resemblance to the head of a nereid polychaete worm (see Brusca and Brusca, 1990:383; Fig. 18): "I will not conceal that the whole arrangement has above all produced a 'mimetic' impression upon me, as if it were intended to resemble, e.g., the head of a Nereid; and I have been compelled to think of the old notions of the employment by the fishing-frog [*Lophius*] of its homologous frontal appendage as a means of attracting other fishes, which indeed, have given origin to its scientific specific name [*piscatorius*]."

Clarke (1878:243), in describing what is now called *Himantolophus appellii* (Fig. 12), agreed with Lütken's assessment: "The probable use of the tentacular appendage as an attractive lure, is beyond conjecture, as the habits of an allied fish (the

angler), which is supplied with a far less complicated attachment, have been closely studied and provided to be 'a fish which angles for fish,' with a natural rod, line, and bait, and with certainly as deadly a 'creel' as any human disciple of Isaac Walton might have to which to relegate its captives."

While offering an alternative hypothesis for the function of the first dorsal-fin spine, Sir Wyville Thomson (1877:68), writing in reference to *Ceratias uranoscopus*, was explicit in describing its habitat as benthic (see also Goode, 1881:469, and Goode and Bean, 1896:490, where this same passage is repeated verbatim, without attribution):

The presence of a fish of this group at so great a depth is of special interest. From its structure, and from the analogy of its nearest allies, there seems to be no reasonable doubt that it lives on the bottom. It is the habit of many of the family to lie hidden in the mud, with the long dorsal filament and its terminal soft expansion exposed. It has been imagined that the expansion is used as a bait to allure its prey, but it seems more likely that it is a sense-organ, intended to give notice of their approach.

A number of other early authors agreed with this bottom-living life-style (e.g., Goode, 1881:469; Gill, 1883: 284; Goode and Bean, 1896:490), but Henri Filhol (1885:81) went a step further when he published an unlikely picture of *Melanocetus johnsonii* in which several individuals (modeled after Günther, 1864, pl. 25) are shown buried up to their eyes in the mud, with their lures waving above their heads (Fig. 19). The fact that the nearly vertical mouth of this species opens upward at a sharp angle makes these fish look rather implausible buried tail-downward in the ooze of the ocean bottom (Waterman, 1939a).

Garman (1899:81), in his original description of *Dolopichthys allector* (Fig. 14), also remarked on the improbability of such fishes being active swimmers, calling them "degenerate pediculates

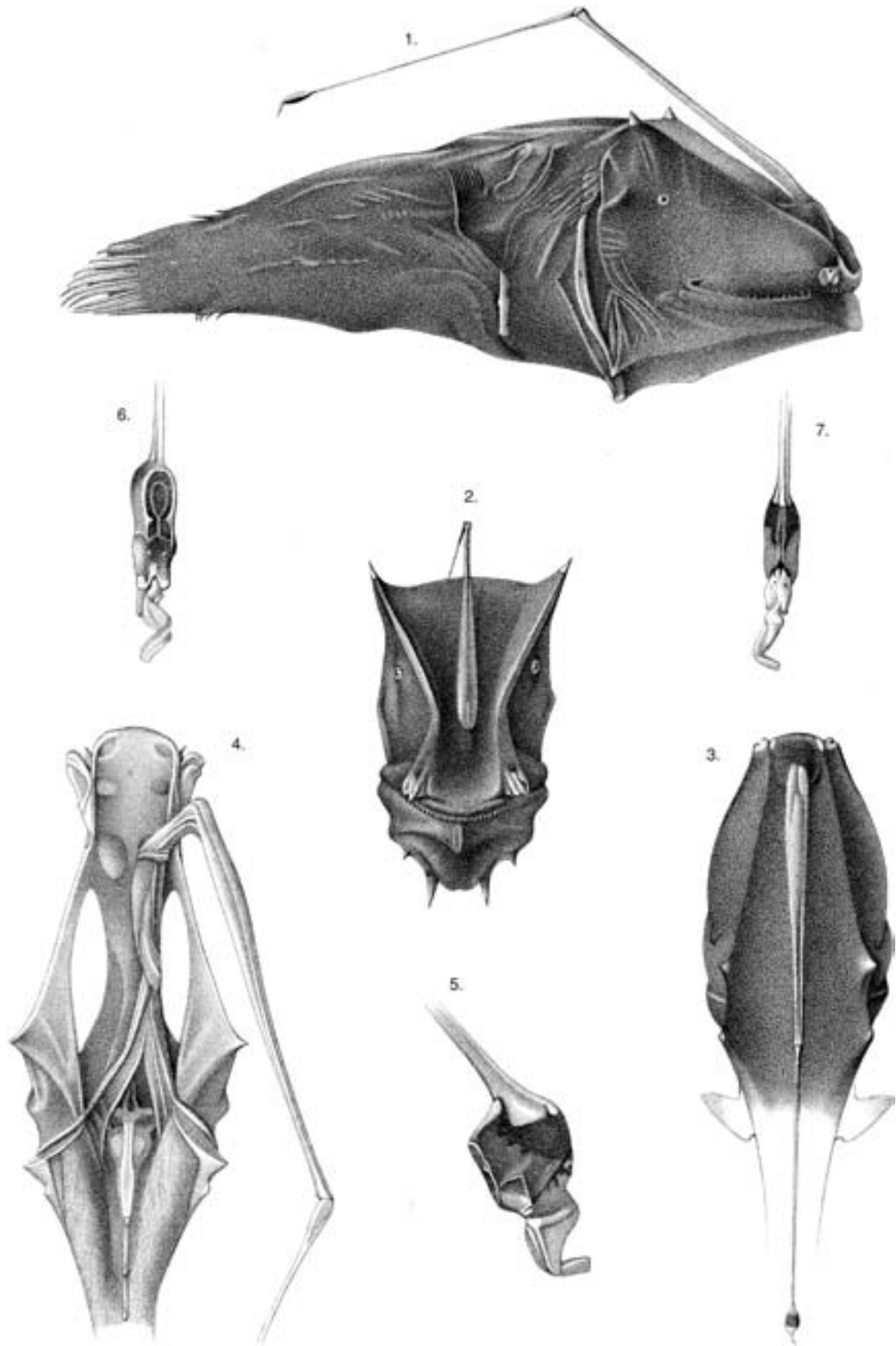


FIGURE 14. Illustrations from Samuel Garman's original description of the holotype of *Dolopichthys allector*, female, 61 mm SL, MCZ 28735: **(1-3)** lateral, anterior, and dorsal views; **(4)** head and body in dorsal view after removal of the skin, showing, among other things, the musculature of the illicial apparatus; **(5-7)** lateral, anterior, and posterior views of the esca. Lithograph by E. Meisel from drawings by A. M. Westergren; after Garman (1899).

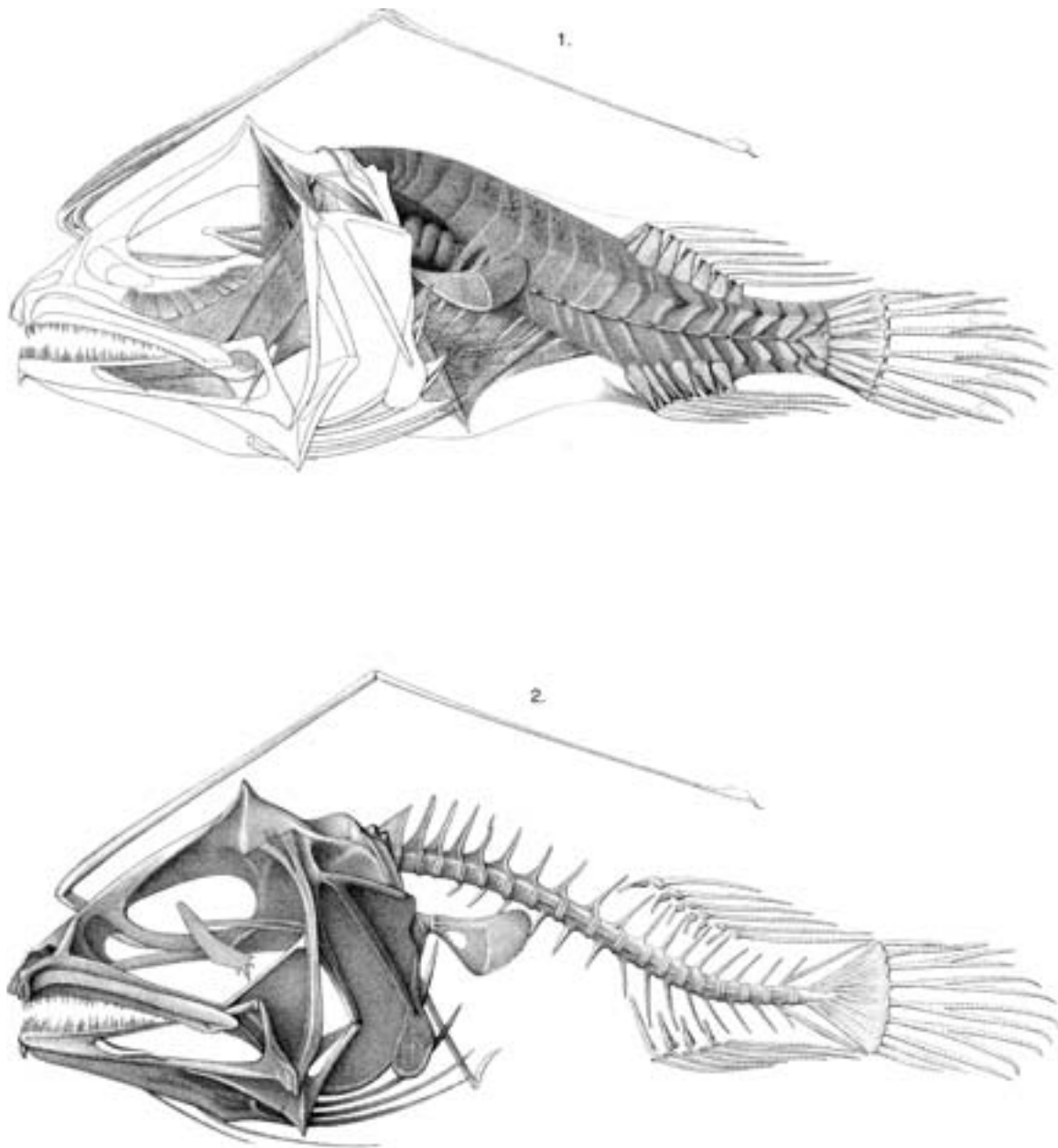


FIGURE 15. More illustrations from Samuel Garman's description of the holotype of *Dolopichthys allector*, female, 61 mm SL, MCZ 28735: (1) muscles and bones of the left side; (2) skeleton after removal of the skin. Lithograph by E. Meisel from drawings by A. M. Westergren; after Garman (1899).

adapted to a life in the mud and ooze at great depths in the ocean, having fins more or less concealed in the skin and imperfectly suited to free progression off the bottom, and capturing prey by means of an illicium, a modification of the anterior dorsal spine. In his use of the word "illicium" for the first dorsal-fin spine, Garman (1899:15, 18, 75–77, 81–83) introduced a new term taken from the Latin, meaning "attraction" or "inducement." At the same time (1899:77, 82), he introduced to modern readers the related term "esca," the Latin word for "bait," which had been used rather frequently by classical Greek and Roman authors (e.g., Cicero, c. 45 BC; see Waterman, 1939a) as well as by the sixteenth-century naturalists (e.g., Rondelet, 1554; see Pietsch and Grobecker, 1987) in their descriptions of the feeding habits of the fishing-frogs (*Lophius piscatorius* and *Lophius budegassa*) of the Mediterranean. The term "illicium" was adopted

rather quickly, first reinforced by Gill (1909) and somewhat later by Regan (1912), who immediately recognized its value, using it later throughout his two monographs on the Ceratioidei (Regan, 1926; Regan and Trewavas, 1932). In contrast, and for some unknown reason, the equally useful expression "esca" was slow to be accepted. In fact, no one after Garman (1899) seems to have used it, except Gill (1909) who gave brief mention, and subsequently by Waterman (1939a, 1939b) who reintroduced it and applied it to his original descriptions of *Gigantactis longicirra*, *Linophryne algibarbata*, and *Danaphryne nigrifilis*. But even then the term was not picked up for another decade, until Bertelsen (1951) used it throughout his worldwide revision of the suborder. Since that time, "esca," along with the previously accepted term "illicium," have become standards in describing anglerfish morphology.

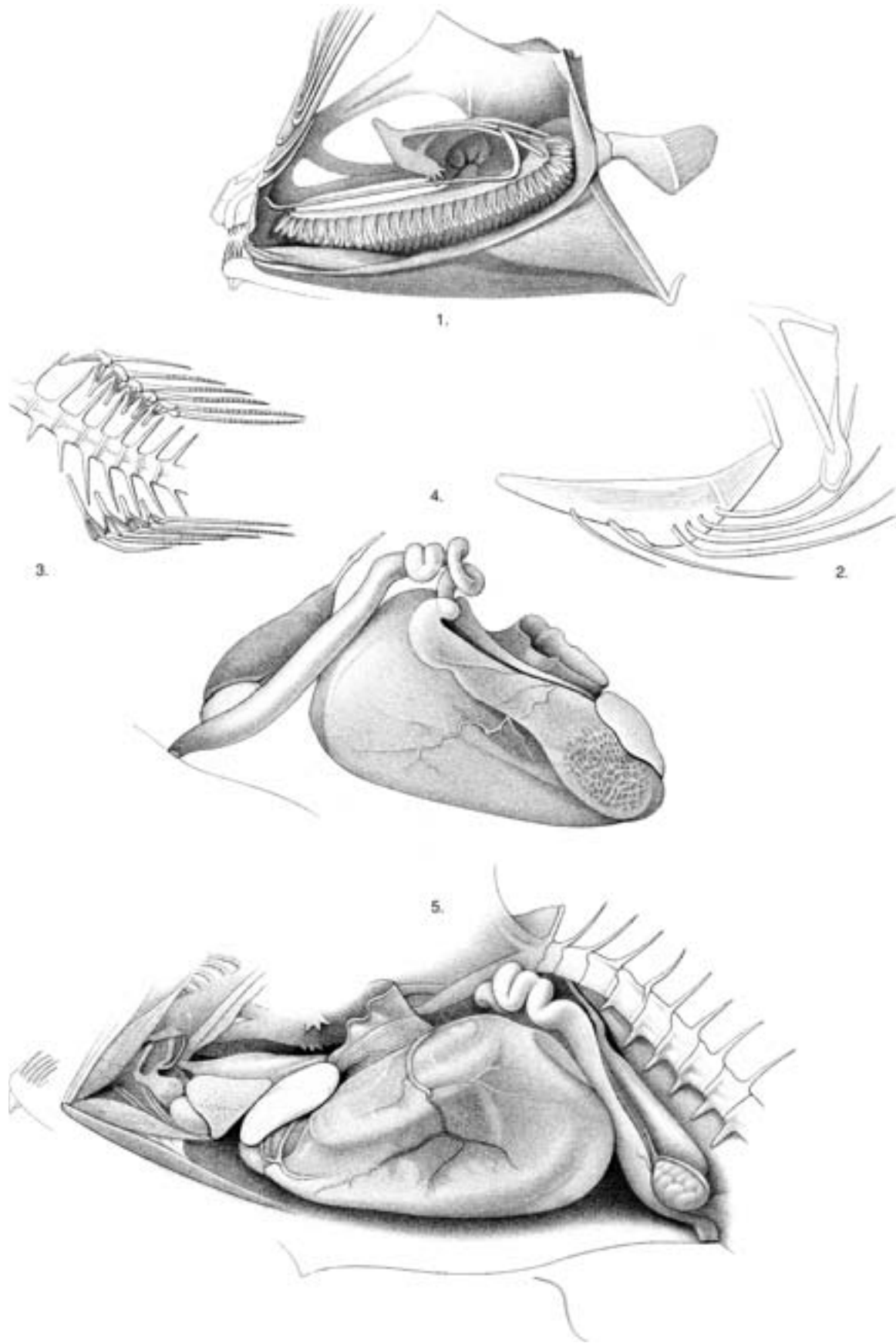


FIGURE 16. More illustrations from Samuel Garman's description of the holotype of *Dolopichthys allector*, female, 61 mm SL, MCZ 28735: **(1)** longitudinal section of the head, showing the gills and gill arches; **(2)** branchiostegal rays, hyoid apparatus, and shoulder girdle; **(3)** bones of the dorsal and anal fins; **(4)** stomach and intestine as viewed from the right side; **(5)** viscera as viewed from the left side. Lithograph by E. Meisel from drawings by A.M. Westergren; after Garman (1899).





FIGURE 17. Charles Tate Regan (1878–1943), renowned ichthyologist and director of the British Museum (Natural History), London. He singled out his discovery of dwarfed males and sexual parasitism in ceratioids as one of his major contributions to ichthyology, a finding that gave him special pleasure and satisfaction (see Burne and Norman, 1943:415). Courtesy of James Maclaine, Jamie Owen, and the Natural History Museum, London.

It was Brauer (1906) who first showed that the ceratioids were meso- and bathypelagic rather than bottom-living forms. He based his conclusion primarily on an analysis of discrete depth samples taken by a vertical closing trawl employed by the German research vessel *Valdivia* in 1898–1899, one of the earliest efforts to retrieve accurate depth distributions of organisms in deep oceanic waters. Brauer further pointed out that several ceratioids in the *Valdivia* collections were found with myctophiform and other pelagic fishes in their stomachs. We know now that ceratioid larvae generally occur at depths of less than 30 m and rarely below 200 m. The onset of metamorphosis leads to a rapid sinking to great depths, so that metamorphosis of females takes place at 2000–2500 m. Young juvenile females are most abundant at slightly shallower depths, 1500–2000 m, while older females seek slightly greater depths and are most common at about 2000 m (Bertelsen, 1951). In addition to the truly benthic ceratioid genus *Thaumatichthys* (see Bertelsen and Struhsaker, 1977), first discovered during the Danish *Galathea* Deep-Sea Expedition of 1950–1952, it is now understood that certain other ceratioid species associate with the bottom. Members of the diceratiid genera *Diceratias* and *Bufoceratias* are more often than not collected in bottom trawls, and benthic organisms have been found in their stomachs (Grey, 1959; Trunov, 1974; Uwate, 1979; Bertelsen, 1990; Anderson and Leslie, 2001; Pietsch et al., 2004:105). An unknown species of *Gigantactis* was recently videotaped from a submersible, swimming upside-down and apparently luring prey from soft muddy bottoms at a depth of 5000 m (Marzuola, 2002; Moore, 2002; see Locomotion, Food, and Feeding, Chapter 7).

Of special importance to the understanding of ceratioid biology (as pointed out by Bertelsen, 1951) were the 1927 and 1930 publications of Albert Eide Parr (1890–1991). Based primarily on material collected during the oceanographic expeditions of the *Pawnee* and funded by the Bingham Oceanographic Foundation of Yale University, Parr (1927) was the first to demonstrate explicitly that esca morphology provides valuable characters for distinguishing species. He provided accurate descriptions and figures of this structure in introducing eight new species based on females, four of which are still recognized today (Fig. 20). In a subsequent publication, Parr (1930a) presented an osteological account of a specimen he called *Rhynchoceratias longipinnis*, comparing it to other forms then included in the Aceratiidae. Although his descriptions were detailed and accurate, “his attempt at a classification of the Aceratiids can only be regarded as evidence of the uncertainty of the correct placing of these fishes at that time” (Bertelsen 1951:8). However, later in that same year, he (Parr, 1930b) found the key to the problem, showing that the specimen he had described earlier was a male with well-developed testes. He indicated the similarity between the known parasitic males and the aceratiids and suggested that all the latter are free-living stages of males, while all other ceratioids, which bear an illicium, are females:

Shortly after having finished a study of the osteology of various genera of the aceratiid family of ceratioid deep-sea fishes, the writer [Parr] was, by general considerations, led to suspect that the family in question might in reality represent merely the free-living stages of the males which have heretofore only been known to science through Mr. C. Tate Regan’s amazing discoveries of various more or less degenerate specimens attached in a presumably parasitic fashion to the skin of the much larger females. No such large females have ever been found in the family Aceratiidae; the latter, on the contrary, are exclusively known from a considerable number and variety of very small forms comparing very well with the parasitic males in regard to size. (Parr, 1930b:129)

Regan and Trewavas (1932) showed that it was now possible, based on Parr’s (1930b) supposition, to place almost all the known free-living males within 5 of the 10 families then recognized on the basis of females (see Part 2, under Reallocation of Nominal Species of Ceratioids Based on Free-living Males). Their systematic revision of the suborder was based on a series of fundamental osteological characters common to all males and females of the same family, but which could not be used to establish taxonomic subunits within the families (Bertelsen, 1951). The free-living males were therefore referred to their own genera, separate from those based on females. Regan and Trewavas (1932:20) pointed out that two “male species,” *Haplophryne mollis* and *Aceratias macrorhinus*, closely resemble the parasitic males of the “female genera” *Edriolychnus* and *Borophryne*, respectively. Because of the extreme sexual dimorphism, generic and specific divisions within the families were based on secondary sexual characters, with the result that the taxonomy of the females and males was radically different. In no case was there any agreement between the number of female and male genera and species within a given family. For example, two families, the Melanocetidae and Himantolophidae, each contained a “female genus” and two “male genera,” and the number of species based on males was likewise greater than that of the females. On the other hand, Regan and Trewavas (1932:20) divided the Oneirodidae into 11 “female genera” containing 42 species, but only a single “male genus” with three species; two “male species” were placed within a separate family, the Laevoceratiidae, as types of separate genera.

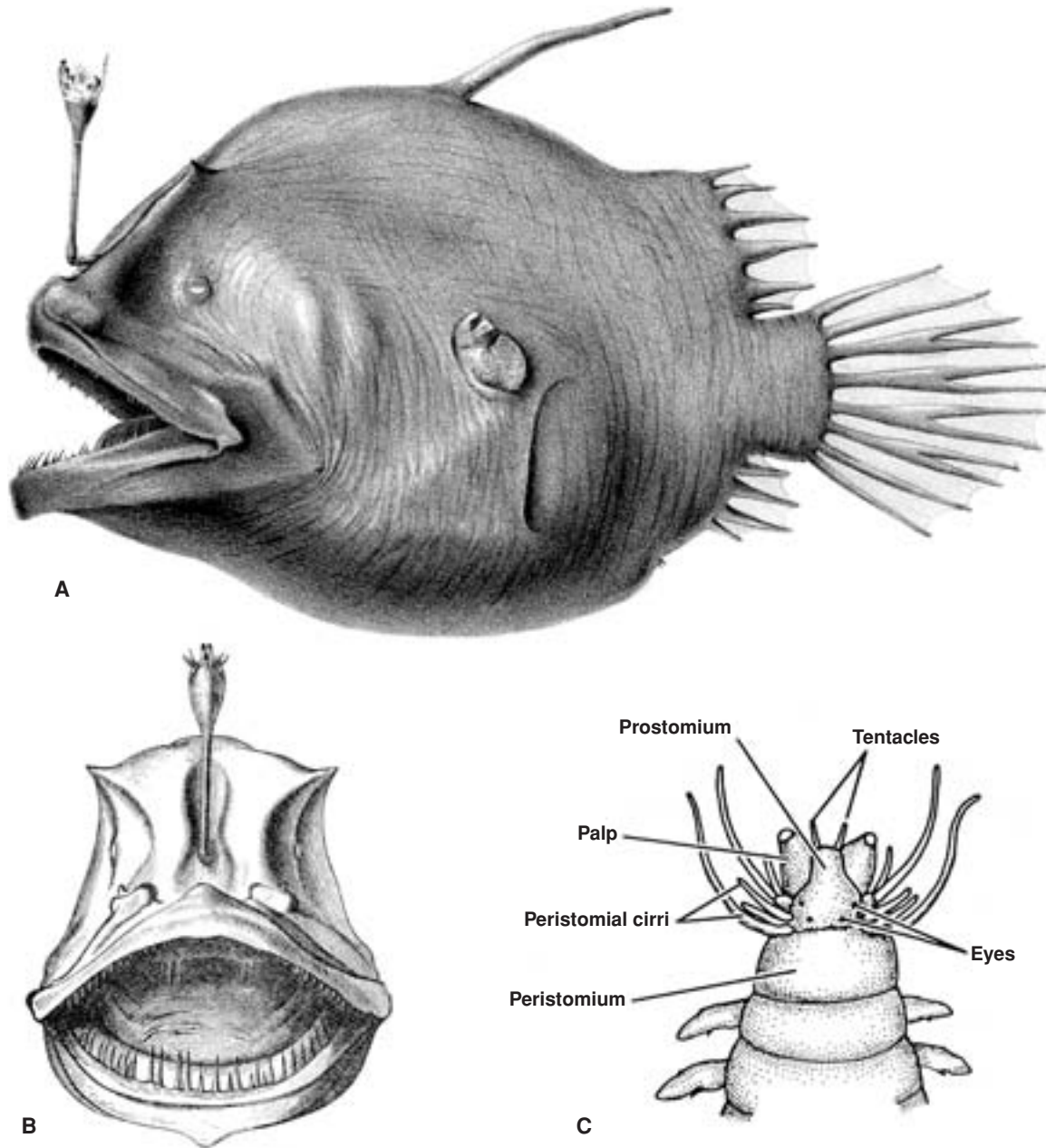


FIGURE 18. The holotype of *Oneirodes eschrichtii*, 153 mm SL, ZMUC 64, taken from Lütken's original description of 1871: (A, B) lateral and anterior views; (C) head of a nereid polychaete worm, after Brusca and Brusca (1990). To better attract prey, Lütken (1871) imagined that the esca might mimic the head of the worm, but this seems unlikely—most nereids and, for that matter, most polychaetes are epibenthic in shallow inshore waters, never living sympatrically with ceratioids.

Such was the taxonomic confusion that faced Erik Bertelsen as he began his studies of the Ceratioidei in the early 1940s. Well aware that not all ceratioid species were known, he described the misfit between the number of genera and species as

so great that we cannot ascribe it to faulty representation. So far as the free-living males are concerned, the nomenclature must be regarded as purely provisional. Both genera and species are exclusively defined by characters whose variation and consequent taxonomic value are entirely or almost unknown. On the whole, the female genera seem particularly well defined, but the separation of the species is often based on such small differences between so few specimens that it simply rests on a subjective estimate, whether they may be considered justifiable. (Bertelsen, 1951:8)

Erik Bertelsen's (Fig. 21) enormous contribution to our knowledge of ceratioid anglerfishes is founded primarily on a detailed examination of some 2400 larvae in the *Dana* collections. The objectives of his investigation, published in 1951, were to (1) sort the material into the lowest possible taxonomic units; (2) place these groups within the existing taxonomic hierarchy of juveniles and adults; (3) describe the ontogeny of the various constituent taxa; (4) resolve the relationship between metamorphosed free-living males and females (which had heretofore been placed in separate genera); and (5) add to the body of information regarding the extraordinary biology of these fishes, especially the related phenomena of male dwarfism and sexual parasitism. While impractical to list all of his findings here, a brief summary follows:

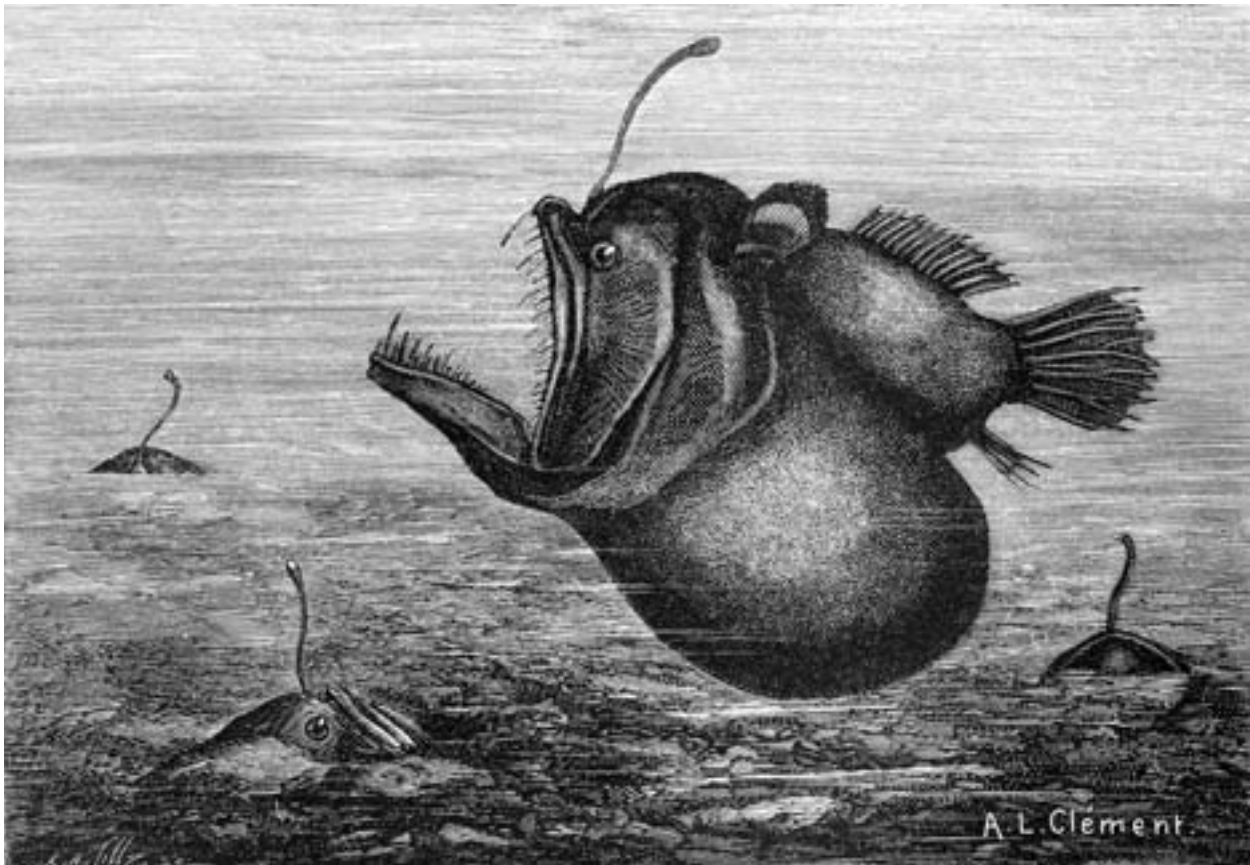


FIGURE 19. An imaginative view of a population of *Melanocetus johnsonii* living in the abyssal ooze published by Henri Filhol (1843–1902), professor of paleontology at the Jardin des Plantes, Paris, in his *La Vie au Fond des Mers (Life at the Bottom of the Seas)*. After Filhol, 1885.

In part one of his monograph, under the heading of “Ontogeny and Taxonomy,” Bertelsen (1951:7–196) addressed the characters common to both sexes, showing that the osteological features that define families and genera can “as a rule” be determined in the larvae by examination of cleared and alizarin-stained specimens. He also showed that the pattern of subdermal pigmentation, which is genus specific, and in some taxa even species specific, is laid down in the smallest larvae and retained subdermally for some time following metamorphosis and may be recognized in most males and juvenile females. Thus, with this new body of information, coupled with an analysis of fin-ray counts, Bertelsen was able to link not only the larvae to families and genera based on females, but most of the free-living males as well.

As for secondary sexual characters, Bertelsen demonstrated among other things that the presence or absence of an illicium can be determined in the youngest of larvae. He found also that a size difference between the sexes becomes apparent at or immediately before metamorphosis, and that in early metamorphosis the shape of the body diverges, the head of the female increasing greatly in relative size, especially the jaw apparatus, while the male becomes more slender and its head and jaws decrease in relative size. He determined also that ceratioid males, even as larvae, show no indication of having light organs of any kind, while the light organ of the esca of females is laid down in the larval stage and is present in all metamorphosed females, with the exception of two genera, *Caulophryne* and *Neoceratias*. The eyes of the larvae are well developed and relatively largest in the smallest individuals. After metamorphosis, the eyes of the females of all families grow very little

and are relatively tiny and vestigial in the largest adult specimens. In contrast, development of the eyes of the males is highly variable among families: they become vestigial in gigantactinids; small in centrophrynids and diceratiids; relatively large and provided with an aphakic space (a space anterior to the edge of the lens that has no focusing element, thought to enhance the forward binocular field of vision; see Schwab, 2004) in caulophrynids, melanocetids, himantolophids, and oneirodids; very large and bowl shaped, with a pupil diameter twice as large as the lens in ceratiids; and “telescopic” in linophrynids. The olfactory organs of the larvae and metamorphosed females are small, but in older larvae they are generally larger in males than in females. Except in the ceratiids (and perhaps neoceratiids), the olfactory organs of the males grow enormously during and after metamorphosis.

A detailed study of the ontogeny of ceratioids, and identification of the free-living males that had previously been placed in their own genera separate from the females, provided the materials for a full taxonomic revision of the suborder (Bertelsen, 1951). The number of families was reduced from 11 to 10: the family Laevoceratiidae was rejected, the Photocorynidae included in the Linophrynidae, and a new family, the Centrophrynidae, added. Hypotheses of evolutionary relationship were proposed for the first time: the Caulophrynidae was given the “most primitive position,” based on, among other things, the discovery of pelvic fins in the larval stages. Seventeen genera were synonymized and 5 new ones erected (based on earlier described species), reducing the total number from 46 to 34. Three of the 34 genera were retained provisionally until such time that the males could be studied and

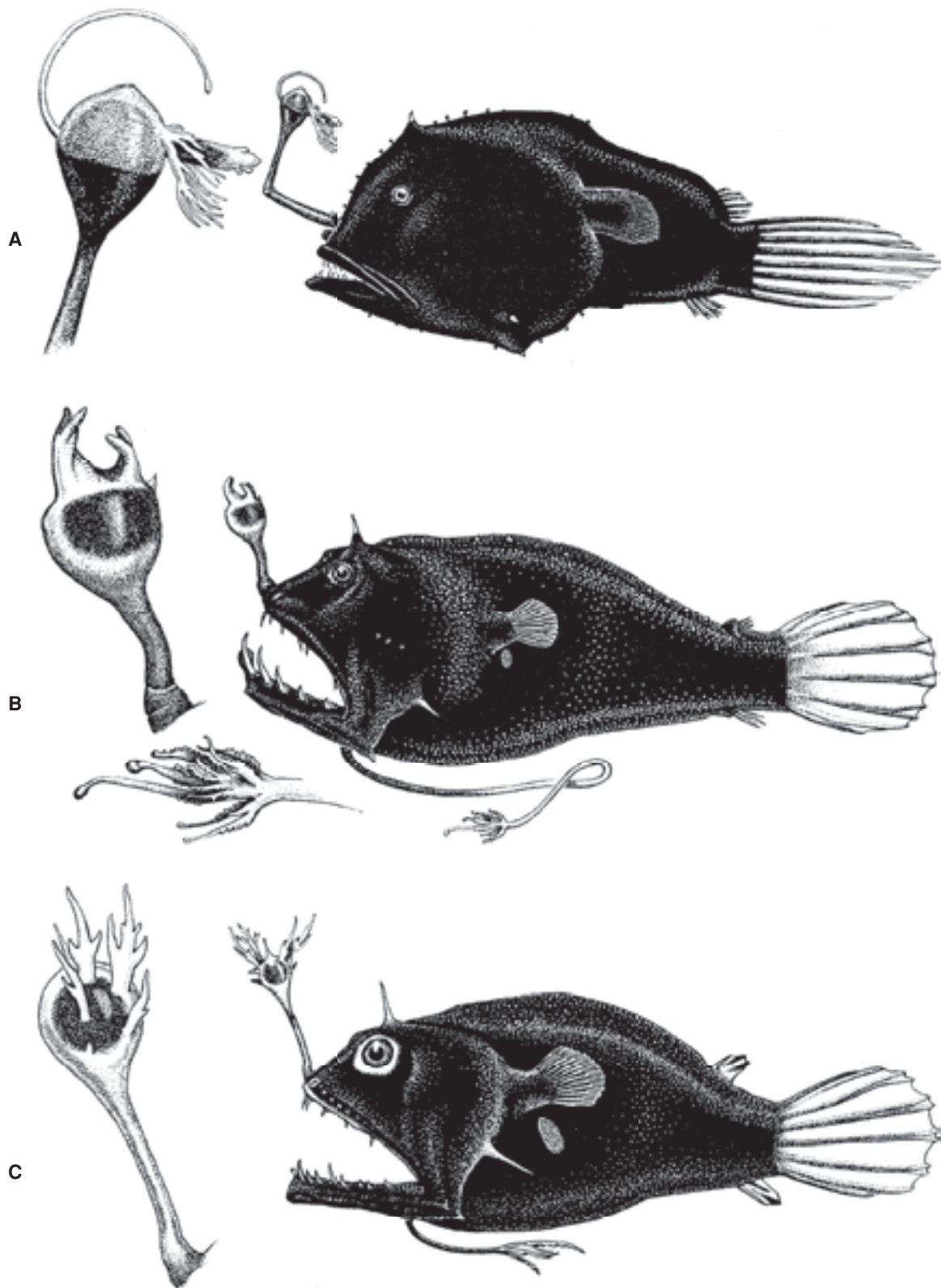


FIGURE 20. New species of ceratioid anglerfishes described by Albert Eide Parr (1890–1991) of Yale University, as a result of the Third Oceanographic Expedition of the yacht *Pawnee* under the direction of Harry Payne Bingham (1887–1955), philanthropist, sportsman, art patron, and founder of the Bingham Oceanographic Foundation of Yale University: **(A)** *Dolopichthys obtusus*, female, 13 mm SL, YPM 2028, now recognized as a junior synonym of *Oneirodes eschrichtii*; **(B)** *Linophryne coronata*, female, 33 mm SL, YPM 2005; **(C)** *Linophryne brevibarbis*, female, 25 mm SL, YPM 2001, a junior synonym of *Linophryne macrodon*. Drawings by Wilfrid S. Bronson; after Parr (1927).



FIGURE 21. Erik Bertelsen (1912–1993), celebrated ichthyologist, fisheries biologist, and the all-time world authority on the Ceratioidei, shown here having fun aboard the Russian Research Vessel *Vitiaz*, 29 November 1988 (for a tribute to his life, see Nielsen, 1994). Courtesy of Jørgen Nielsen, Peter Rask Møller, and the Zoological Museum, University of Copenhagen.

identified. Of the more than 200 nominal species of ceratioids, which by 1951 had been reduced to 178 by various authors, Bertelsen rejected 61 and added 2 new ones, for a total of 119. Unable to revise certain species-rich genera (e.g., *Oneirodes*) for a lack of adequate comparative material, and acknowledging that a number of species based only on males must be regarded as provisional, he concluded that the known material of the suborder represents no more than 80 species.

Prior to Bertelsen's (1951) monograph, the scientific literature contained descriptions or mention of only about 50 ceratioid larvae. Among this material, representatives of four families were correctly referred to family, but only two genera and not a single species were correctly identified. In contrast, based on the approximately 2400 larvae in the *Dana* collections, Bertelsen recognized and described the early development of 30 taxa. Nineteen of these were identified with their respective species, three were referred to a group of species within a genus, seven could be identified only to genus, and one only to family. His descriptions of the larvae included representatives of all 10 families and 22 of the 34 genera then recognized.

Also prior to Bertelsen's (1951) work, the known free-living males were, with some few exceptions, correctly referred to 4 of the 10 families of the suborder, one was wrongly placed in a fifth family, and two were provisionally placed in the now discarded Laevoceratidae. None was referred to a species based on females, and, apart from a few uncertain suppositions, only one was (but incorrectly) referred to a genus that also contained females. Of the 166 metamorphosing or metamorphosed free-living males in the *Dana* collections, 63 had been previously described by Regan (1926) and Regan and Trewavas (1932). In addition to representatives of the families Himantolophidae,

Melanocetidae, Oneirodidae, and Linophrynidae to which Regan and Trewavas had already referred specimens, Bertelsen was able to assign free-living males to the Centrophrynidae and Gigantactinidae, the males of which had been unknown previously; as well as to the Caulophrynidae and Ceratiidae, whose males had previously been known only as parasites on females. Of the two remaining families, Neoceratiidae and Diceratiidae, the males of which had been previously unknown, he described a parasitic male of the first, and to the other he referred the free-living male *Laevoceratias liparis* that had been described by Parr (1927). The males examined by Bertelsen were divided into 27 taxa, all of which were referred to genera based on females; 14 of these were further identified to species based on females.

Part two of Bertelsen's (1951:197–251) monograph is devoted to an analysis of "Distribution, Ecology, and Biology." Thanks to the methodical and well-defined collecting protocols employed by the scientific crew of the *Dana* expeditions—but limited primarily to collections made in the North Atlantic—he was able to provide the first quantitative study of the seasonal, vertical, and horizontal distribution of ceratioids. At the same time, based on their anatomy, stomach contents, analyses of catch data, and the small and infrequent information on the behavior of specimens that lived a short time after capture, he provided an account of their ecology and general biology, including a discussion of their swimming powers, bioluminescence, food habits, and reproduction, the latter in special reference to sexual dimorphism and parasitism. In summary, Bertelsen's great work set the standard and laid the foundation for all future studies of this enigmatic group of fishes for the next half century.

In 1968, through the intermediacy of my major professor, Basil G. Nafpaktitis, who guided me with great care and expertise through the travails of graduate school, I was extremely fortunate to become closely associated with Erik Bertelsen, whose name was and still is synonymous with "Ceratioidei," at least among ichthyologists. Beginning at this early time, and during the 25 years that followed, Bertelsen and I undertook a program of systematic studies of ceratioid genera and families, sometimes working alone, independently, but more often together. In addition to a few small papers beginning in 1969, some of which described new ceratioid genera (Pietsch 1969, 1972b, 1973), I reviewed the Centrophrynidae (1972a), based on new material collected from the Gulf of California. Following shortly thereafter, I published revisions of the oneirodid genera *Dolopichthys* (1972c), *Oneirodes* (1974a), *Lophodolos* (1974b), *Chaenophryne* (1975b), the so-called long-pectoral oneirodid genera (i.e., *Leptacanthichthys*, *Chirophryne*, *Ctenochirichthys*, and *Puck*; 1978), and the families Caulophrynidae (1979) and Ceratiidae (1986b).

Bertelsen, during this same time period, produced independently seven revisionary papers on the Linophrynidae (1973, 1976, 1978, 1980a, 1980b, 1981, 1982), continuing a numbered series of publications on this family that he had started in 1965, the first in collaboration with the late Gerhard Krefft (Fig. 22). Also produced by Bertelsen during these years were two remarkably detailed and beautifully illustrated monographs: the first, a review of the genus *Thaumatichthys*, in coauthorship with Paul J. Struhsaker (1977), and second, a revision of the family Himantolophidae, with Krefft (1988).

As for Bertelsen and Pietsch together, our first collaboration was a review of the oneirodid genus *Spiniphryne* (1975), based on new material collected by the research cruises of the German FRV *Walther Herwig* off South America. This was followed



FIGURE 22. Erik Bertelsen with his long-time friend and collaborator Gerhard Krefft (1912–1993), ichthyologist, fisheries biologist, and founder of the great collection of marine fishes at the Institut für Seefischerei (ISH) in Hamburg, which was transferred to the Zoological Museum of the University of Hamburg in 1993 shortly after Krefft's death (for more on his life, see Stehmann and Hulley, 1994, and Stehmann, 1997). Photograph taken in Krefft's office at ISH, 12 December 1985; courtesy of Jørgen Nielsen, Peter Rask Møller, and the Zoological Museum, University of Copenhagen.

shortly thereafter by a review of the oneirodids resulting from those same expeditions (1977), a paper describing the ceratioid anglerfishes of Australia (1983), a revision of the family Gigantactinidae (with Robert J. Lavenberg, 1981), a “resurrection of the ceratioid anglerfish *Ceratias tentaculatus*” (1984), and three studies completed and published posthumously: a revision of the thaumatichthyid genus *Lasiognathus* (1996), a revision of the gigantactinid genus *Rhynchactis* (1998), and a new species of *Gigantactis* (2002).

Au:  
Bertelsen  
& Pietsch  
1998a or  
b?

Despite this flurry of activity during the 1970s, 1980s, and 1990s, during which time all major taxa of the Ceratioidei were either reviewed or revised, and four genera and 66 species were described as new to science, we are not yet close to knowing the full diversity of ceratioids. Of the 160 species recognized in this monograph, 23, or about 14%, are still known only from the holotype, 53 (33%) are known from three female specimens or fewer, and only 84 species (52%) are represented by more than six females. Consequently, knowledge of individual, ontogenetic, and geographic variation is extremely limited. While the taxonomy of females is poorly known, that of males is much worse: only 29 of the 160 species are represented by males, and by far most of these are identified with species based on females only because they belong to monotypic genera or because they are parasitically attached to females; the hundreds of males in collections around the world, if identified at all, are still named only to genus. The rate of description of new species, while characterized by occasional large spikes that coincide with major revisions (e.g., Regan, 1925b; Regan and Trewavas, 1932; Pietsch, 1974a; Bertelsen, 1980a, 1980b, 1982; Bertelsen et al., 1981; Bertelsen and Krefft, 1988), has not lev-

eled off despite steeply declining exploratory fishing activity around the world in the past 20 years (Bertelsen, 1982; Mihai-Bardan, 1982; Bertelsen and Pietsch, 1983, 1996, 1998, 2002; Kharin, 1984, 1989; Balushkin and Fedorov, 1985, 1986; Leipertz and Pietsch, 1987; Balushkin and Trunov, 1988; Bertelsen and Krefft, 1988; Ni, 1988; Swinney and Pietsch, 1988; Orr, 1991; Gon, 1992; Stewart and Pietsch, 1998; Ho and Shao, 2004; Pietsch, 2004, 2005a, 2005b, 2007; Pietsch et al., 2004; Pietsch and Baldwin, 2006).

Au: Ber-  
telsen &  
Pietsch  
1998a or  
b?

This monograph is by no means the last word on this extraordinary group of animals. The descriptive phase of our knowledge of ceratioids, and deep-sea biology in general, is not over and may well be still in its early stages. New species will continue to be discovered, and the filling of taxonomic gaps will provide new insights into phylogenetic relationships. The addition of new material will expand our knowledge of geographic distributions, both horizontal and vertical. Observations of freshly caught specimens, and in situ sightings from remote and manned submersibles will provide new information about behavior. Resolving the seemingly insurmountable problems of keeping ceratioids alive after capture will lead eventually to exhibits in public aquaria, which may in turn provide new insights into the unique reproductive modes of these fishes, sexual parasitism, and the intriguing biomedical implications of tissue compatibility.

Acknowledging that much more remains to be learned, I hope that what is presented in this volume is as correct and as complete as possible, and that where I have made decisions, they have been as objective as possible. Time will tell, and such errors as may come to light will be my responsibility alone.