

# Dimorphism, parasitism, and sex revisited: modes of reproduction among deep-sea ceratioid anglerfishes (Teleostei: Lophiiformes)

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**Abstract** Sexual parasitism, a remarkable mode of reproduction unique to some members of the deep-sea anglerfish suborder Ceratioidei, in which males are dwarfed and become permanently attached to much larger females, is described in a number of previously unreported specimens and taxa. Although generally attributed to all ceratioids, and despite more than a sevenfold increase in the number of known parasitized females in collections throughout the world in the past 50 years, the phenomenon is surprisingly confined to few taxa within the suborder. To date, permanently attached males have been found in only 5 of the 11 ceratioid families, 10 of the 35 genera, and 23 of the 160 recognized species. Notes on taxonomic content, available material, occurrence of sexual parasitism, gravid females and ripe males, the development of eyes and nostrils of the males, the ability of males to capture and ingest food independently of the female, occurrences of multiple attachments of males to a single female, and the nature of the fusion between coupled males and females are given for each ceratioid family. This information is then summarized and discussed. Evidence is presented to reaffirm the presence of three reproductive modes: obligatory parasitism, facultative parasitism, and temporary nonparasitic attachment. Additional evidence is provided to reaffirm the hypothesis that sexual parasitism has evolved separately at least three and perhaps five or more times within the suborder.

**Key words** Teleostei · Lophiiformes · Ceratioidei · Anglerfishes · Deep sea · Reproductive strategies · Sexual dimorphism · Sexual parasitism

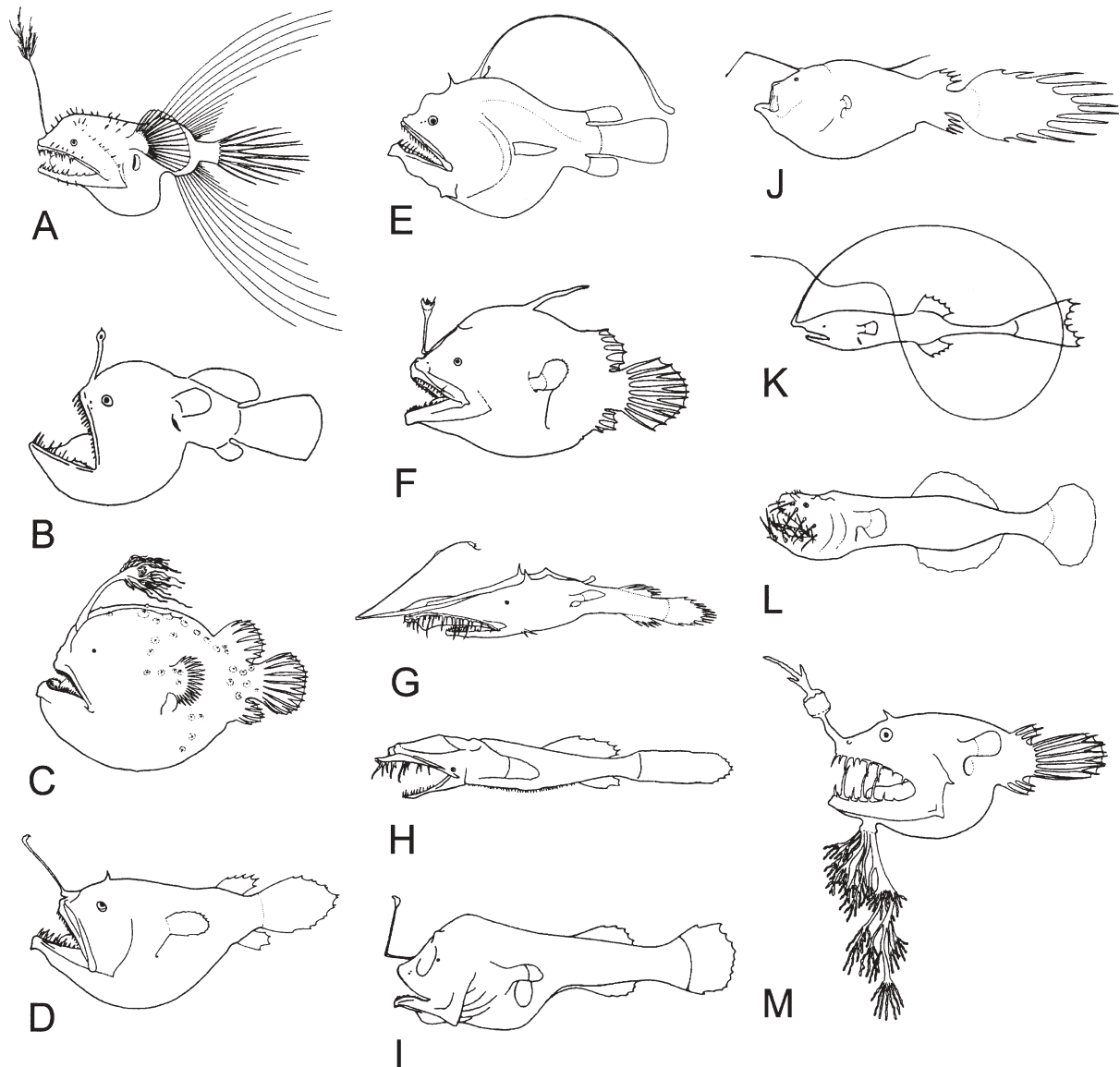
*To be driven by impelling odor headlong upon a mate so gigantic, in such immense and forbidding darkness, and willfully to eat a hole in her soft side, to feel the gradually increasing transfusion of her blood through one's veins, to lose everything that marked one as other than a worm, to become a brainless, senseless thing that was a fish—this is sheer fiction, beyond all belief unless we have seen the proof of it.*

William Beebe, 1938

**A**nglerfishes of the suborder Ceratioidei, constituting the most phylogenetically derived member of the teleost order Lophiiformes (Bertelsen, 1984; Pietsch, 1984; Pietsch and Grobecker, 1987), are distributed throughout the world's oceans below a daytime depth of 300 m. With 160 currently recognized species, distributed among 11 families (Fig. 1), it is by far the most species-rich vertebrate taxon within the bathypelagic zone, containing more than twice as many families and genera and more than three times the number of species as the Cetomimoidei, the next most species-rich bathypelagic vertebrate taxon (see Paxton, 1998: 163; Herring, 2002: 232). 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 (lophioids, antennarioids, chaunacoids, and ogocephaloids) 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 linophryniids, adults at 6–10 mm standard length, competing for the title of world's smallest vertebrates (see Winterbottom and Emery, 1981; Roberts, 1986; Weitzman and Vari, 1988; Kottelat and Vidthayanon, 1993; Watson and Walker, 2004)—and attach themselves (either temporarily or permanently) to bodies of relatively gigantic females. In *Ceratias holboelli*, 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: 15). The males lack a luring apparatus and those of most species are equipped with large well-developed eyes (Munk, 1964, 1966) and relatively huge nostrils (Marshall, 1967a,b), the latter apparently used for homing in on a female-emitted, species-specific pheromone (Bertelsen, 1951; Pietsch, 1976; Munk, 1992). Normal jaw teeth are lost during metamorphosis, but are replaced by a set of pincer-like denticles (denticular bones of Bertelsen, 1951; 21–22, figs. 5, 6) at the anterior tips of the jaws for grasping and holding fast to a prospective mate.

In some taxa, attachment is followed by fusion of tissues and apparently by a 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 (for



**Fig. 1.** Representative females of families of the Ceratioidei. **A** Caulophryniidae; **B** Melanocetidae; **C** Himantolophidae; **D** Diceratiidae (*Bufoceratias*); **E** Diceratiidae (*Diceratias*); **F** Oneirodidae; **G** Thaumatchthyidae (*Lasiognathus*); **H** Thaumatchthyidae (*Thaumatchthys*); **I** Centrophryniidae; **J** Ceratiidae; **K** Gigantactinidae; **L** Neoceratiidae; **M** Linophryniidae

example, see Regan, 1925a,b; Regan and Trewavas, 1932; Bertelsen, 1951; Pietsch, 1976; 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 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 so 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 (Table 1). Since its discovery some 80 years ago (Saemundsson, 1922; Regan, 1925a,b), the story of sexual parasitism in ceratioid anglerfishes has become a part of common scientific knowledge. However, the known facts concerning this remarkable reproductive mode have never been thoroughly and satisfactorily analyzed, despite the elegant work of Bertelsen (1951) and more recently of Munk and Bertelsen (1983) and Munk (2000).

**Table 1.** Records of attached males of Ceratioidei in collections around the world

Family	Genus	Species	Female	Male(s)	Author and date	Catalog number
Caulophrynidae	<i>Caulophryne</i>	<i>polynema</i>	142 mm	16 mm	Regan, 1930a,b	BMNH 1930.2.7.1
	<i>Caulophryne</i>	<i>polynema</i>	137 mm	15 mm	Unpublished	MNHN 2001-140
	<i>Caulophryne</i>	sp.	98 mm	12 mm	Pietsch, 1979	LACM 36025-1
Melanocetidae	<i>Melanocetus</i>	<i>johnsonii</i>	75 mm	23.5 mm	Unpublished	BMNH 2004.6.3.2-3
	<i>Melanocetus</i>	<i>murrayi</i>	73 mm	15 mm	Unpublished	BSKU 57842
Oneirodidae	<i>Bertella</i>	<i>idiomorpha</i>	77 mm	11 mm	Unpublished	UW 48712
	<i>Leptacanthichthys</i>	<i>gracilispinis</i>	56 mm	7.5 mm	Pietsch, 1976	LACM 33625-2
Ceratiidae	<i>Ceratias</i>	<i>holboelli</i>	690 mm	2 (65–70 mm)	Saemundsson, 1922	IINH/ZMUC P922480 <sup>a</sup>
	<i>Ceratias</i>	<i>holboelli</i>	720 mm	75 mm (detached)	Regan, 1925a,b	BMNH 1924.12.29.1-2
	<i>Ceratias</i>	<i>holboelli</i>	580 mm	86 mm	Saemundsson, 1939	ZMUC P922481
	<i>Ceratias</i>	<i>holboelli</i>	770 mm	118 mm	Bigelow and Barbour, 1944	MCZ 36042 <sup>b</sup>
	<i>Ceratias</i>	<i>holboelli</i>	735 mm	75 mm	Bertelsen, 1951	MRIR <sup>c</sup>
	<i>Ceratias</i>	<i>holboelli</i>	1100 mm TL	80 mm TL	Kreff, 1961	NMH 1-1959
	<i>Ceratias</i>	<i>holboelli</i>	1270 mm TL	160 mm TL	Kreff, 1961	Apparently lost
	<i>Ceratias</i>	<i>holboelli</i>	640 mm	70 mm	Blacker, 1972	BMNH 1970.10.28.20
	<i>Ceratias</i>	<i>holboelli</i>	1000 mm TL	?	Du Buit et al., 1980	MNHN, misplaced
	<i>Ceratias</i>	<i>holboelli</i>	670 mm	97.5 mm	Ni, 1988	ECSFRI
	<i>Ceratias</i>	<i>holboelli</i>	595 mm	70 mm	Amaoka et al., 1995	HUMZ 77841
	<i>Ceratias</i>	<i>holboelli</i>	855 mm	85 mm	Unpublished	BMNH 1953.2.25.1
	<i>Ceratias</i>	<i>holboelli</i>	560 mm	35 mm	Unpublished	CSIRO H.2746-01
	<i>Ceratias</i>	<i>holboelli</i>	690 mm	105 mm	Unpublished	HUMZ 95300
	<i>Ceratias</i>	<i>holboelli</i>	1210 mm TL	190 mm TL	Unpublished	MRIR <sup>d</sup>
	<i>Ceratias</i>	<i>holboelli</i>	980 mm TL	90 mm TL	Unpublished	MRIR <sup>c</sup>
	<i>Ceratias</i>	<i>holboelli</i>	1200 mm TL	?	Unpublished	MRIR <sup>c</sup>
	<i>Ceratias</i>	<i>holboelli</i>	900 mm TL	70 mm TL	Unpublished	MRIR 94-34
	<i>Ceratias</i>	<i>tentaculatus</i>	550 mm	37 mm	Unpublished	CSIRO H.3101-01
	<i>Ceratias</i>	<i>uranoscopus</i>	240 mm	22.5 mm	Pietsch, 1986	LACM 33376-3
	<i>Ceratias</i>	sp.	850 mm TL	38 mm TL	Beebe, 1938	Apparently lost
	<i>Ceratias</i>	sp.	?	?	Matsubara, 1955	Lost; see Abe, 1967
	<i>Ceratias</i>	sp.	650 mm	58 mm	Abe, 1967	Apparently lost <sup>e</sup>
	<i>Ceratias</i>	sp.	460 mm	32 mm TL	Abe, 1967	Apparently lost <sup>e</sup>
	<i>Ceratias</i>	sp.	700 mm	37 mm	Penrith, 1967	SAM 29607
	<i>Ceratias</i>	sp.	525 mm	37 mm	Fitch, 1973	LACM 33718-1
	<i>Ceratias</i>	sp.	212 mm	9.2 mm	Pietsch, 1986	UF 25149
	<i>Ceratias</i>	sp.	370 mm	5-mm remnant	Unpublished	CAS 60358
	<i>Ceratias</i>	sp.	Discarded	73 mm	Unpublished	CAS 82498
	<i>Ceratias</i>	sp.	275 mm	24.5 mm	Unpublished	LACM 36955-1
	<i>Ceratias</i>	sp.	660 mm	46 mm	Unpublished	MNHN 2004-1518
	<i>Ceratias</i>	sp.	740 mm	60 mm	Unpublished	MTF
	<i>Ceratias</i>	sp.	790 mm	2 (65–89 mm)	Unpublished	NMNZ P.40886
	<i>Ceratias</i>	sp.	553 mm	46 mm	Unpublished	UW 22322
	<i>Ceratias</i>	sp.	750 mm	115 mm	Unpublished	ZMH 21014
	<i>Cryptopsaras</i>	<i>couesii</i>	290 mm	12 mm	Tanaka, 1908; Barbour, 1941	MCZ 29855
	<i>Cryptopsaras</i>	<i>couesii</i>	276 mm	12 mm	Abe and Nakamura, 1954	Apparently lost <sup>e</sup>
	<i>Cryptopsaras</i>	<i>couesii</i>	213 mm	2 (27–27.5 mm)	Fast, 1957	SU 49556
	<i>Cryptopsaras</i>	<i>couesii</i>	176 mm	3 (16–37 mm)	Shoemaker, 1958	USNM 177939 <sup>b</sup>
	<i>Cryptopsaras</i>	<i>couesii</i>	272 mm	74 mm	Ueno, 1966; Ueno and Abe, 1967	HUMZ 70815
	<i>Cryptopsaras</i>	<i>couesii</i>	322 mm	41 mm	Penrith, 1967	SAM 23587
	<i>Cryptopsaras</i>	<i>couesii</i>	356 mm	73 mm	Penrith, 1967	SAM 24283
<i>Cryptopsaras</i>	<i>couesii</i>	77 mm	15 mm	Pietsch, 1975	BMNH 2004.6.29.4-5	
<i>Cryptopsaras</i>	<i>couesii</i>	173 mm	35 mm	Pietsch, 1975	LACM 33621-1	
<i>Cryptopsaras</i>	<i>couesii</i>	15.5 mm	9.8 mm	Pietsch, 1975	USNM 234867	
<i>Cryptopsaras</i>	<i>couesii</i>	146 mm	17 mm	Young and Roper, 1977	USNM 219906	
<i>Cryptopsaras</i>	<i>couesii</i>	300 mm	4 (33–60 mm)	Abe and Funabashi, 1992	INM 9201	
<i>Cryptopsaras</i>	<i>couesii</i>	348 mm	3 (54–60 mm)	Amaoka et al., 1995	HUMZ 124596	
<i>Cryptopsaras</i>	<i>couesii</i>	311 mm	40 mm TL	Anderson and Leslie, 2001	SAM 34480	
<i>Cryptopsaras</i>	<i>couesii</i>	343 mm	2 (88–120 mm TL)	Anderson and Leslie, 2001	SAM 34481	
<i>Cryptopsaras</i>	<i>couesii</i>	316 mm	8 (35–56 mm)	Saruwatari et al., 2001	ORIT	
<i>Cryptopsaras</i>	<i>couesii</i>	45 mm	10 mm	Unpublished	ARC 8707665	
<i>Cryptopsaras</i>	<i>couesii</i>	215 mm	44 mm	Unpublished	CAS 73320	
<i>Cryptopsaras</i>	<i>couesii</i>	195 mm	34 mm	Unpublished	CAS 76509	

Table 1. Continued

Family	Genus	Species	Female	Male(s)	Author and date	Catalog number
	<i>Cryptopsaras</i>	<i>couesii</i>	322 mm	51 mm	Unpublished	CSIRO H.2532-02
	<i>Cryptopsaras</i>	<i>couesii</i>	268 mm	36 mm	Unpublished	CSIRO H.4391-01
	<i>Cryptopsaras</i>	<i>couesii</i>	324 mm	48 mm	Unpublished	HUMZ 69165
	<i>Cryptopsaras</i>	<i>couesii</i>	345 mm	6 (18–44 mm)	Unpublished	HUMZ 69166
	<i>Cryptopsaras</i>	<i>couesii</i>	308 mm	4 (78–88 mm)	Unpublished	HUMZ 73014
	<i>Cryptopsaras</i>	<i>couesii</i>	320 mm	48 mm	Unpublished	HUMZ 98265
	<i>Cryptopsaras</i>	<i>couesii</i>	162 mm	24.5 mm	Unpublished	MCZ 164112
	<i>Cryptopsaras</i>	<i>couesii</i>	390 mm	2 (47–99 mm)	Unpublished	NMNZ P.34960
	<i>Cryptopsaras</i>	<i>couesii</i>	252 mm	62 mm	Unpublished	OSUO 12056
	<i>Cryptopsaras</i>	<i>couesii</i>	302 mm	50 mm	Unpublished	SIO 95-30
	<i>Cryptopsaras</i>	<i>couesii</i>	202 mm	20 mm	Unpublished	SIO 97-52
	<i>Cryptopsaras</i>	<i>couesii</i>	94 mm	2 (8.0–14.5 mm)	Unpublished	UF 25157
	<i>Cryptopsaras</i>	<i>couesii</i>	164.5 mm	49 mm	Unpublished	UF 25160
	<i>Cryptopsaras</i>	<i>couesii</i>	108 mm	20.5 mm	Unpublished	UF 25164
	<i>Cryptopsaras</i>	<i>couesii</i>	132 mm	17 mm	Unpublished	USNM 219906
	<i>Cryptopsaras</i>	<i>couesii</i>	215 mm	20 mm	Unpublished	UW 21774
	<i>Cryptopsaras</i>	<i>couesii</i>	240 mm	34 mm	Unpublished	UW 21775
	<i>Cryptopsaras</i>	<i>couesii</i>	230 mm	80 mm	Unpublished	UW 46112
Neoceratiidae	<i>Neoceratias</i>	<i>spinifer</i>	52 mm	15.5 mm	Bertelsen, 1951	ZMUC P921726
	<i>Neoceratias</i>	<i>spinifer</i>	86 mm	17.5 mm	Pietsch, 1976	IOAN
	<i>Neoceratias</i>	<i>spinifer</i>	42 mm	8.5 mm	Pietsch, 1976	LACM 34271-1
	<i>Neoceratias</i>	<i>spinifer</i>	108 mm	18 mm	Pietsch, 1976	SIO 70-336
	<i>Neoceratias</i>	<i>spinifer</i>	77 mm	12.5 mm	Bertelsen and Pietsch, 1983	AMS I.20908-2
	<i>Neoceratias</i>	<i>spinifer</i>	74 mm	12.5 mm	Munk, 2000	ISH 5546/79
	<i>Neoceratias</i>	<i>spinifer</i>	67.5 mm	17.5 mm	Unpublished	SIO 68-478
Linophryniidae	<i>Borophryne</i>	<i>apogon</i>	55 mm	13 mm (detached)	Regan and Trewavas, 1932	ZMUC P92147
	<i>Borophryne</i>	<i>apogon</i>	47 mm	14.5 mm	Regan and Trewavas, 1932	BMNH 1932.5.3.38
	<i>Borophryne</i>	<i>apogon</i>	50 mm	11 mm (detached)	Beebe and Crane, 1947	AMNH 211332
	<i>Borophryne</i>	<i>apogon</i>	51.5 mm	10.5 mm	Beebe and Crane, 1947	Apparently lost
	<i>Borophryne</i>	<i>apogon</i>	65 mm	14 mm	Bertelsen, 1951	ZMUC P921755
	<i>Borophryne</i>	<i>apogon</i>	53 mm	12 mm	Bertelsen, 1951	ZMUC P921756
	<i>Borophryne</i>	<i>apogon</i>	52 mm	12 mm	Kramp, 1953	ZMUC P922322
	<i>Borophryne</i>	<i>apogon</i>	56 mm	9.5 mm	Kramp, 1953	ZMUC P922324
	<i>Borophryne</i>	<i>apogon</i>	60 mm	Tiny remnant	Kramp, 1953	ZMUC P922325
	<i>Borophryne</i>	<i>apogon</i>	101 mm	2 (16–22 mm)	Pietsch, 1976	LACM 30053-10
	<i>Borophryne</i>	<i>apogon</i>	89 mm	20 mm	Pietsch, 1976	SIO 68-112
	<i>Borophryne</i>	<i>apogon</i>	65.5 mm	12 mm	Unpublished	USNM 326570
	<i>Haplophryne</i>	<i>mollis</i>	48 mm	10 mm	Regan, 1925b	ZMUC P92135
	<i>Haplophryne</i>	<i>mollis</i>	50 mm	3 (11–12 mm)	Regan and Trewavas, 1932	ZMUC P921777 <sup>f</sup>
	<i>Haplophryne</i>	<i>mollis</i>	34 mm	11 mm	Regan and Trewavas, 1932	ZMUC P92138
	<i>Haplophryne</i>	<i>mollis</i>	38 mm	2 (9.5–10 mm)	Pietsch, 1976	SOC <sup>g</sup>
	<i>Haplophryne</i>	<i>mollis</i>	40 mm	2 (10.5–11 mm)	Pietsch, 1976	BMNH 2004.8.17.48-50
	<i>Haplophryne</i>	<i>mollis</i>	70 mm	2 (11–12.5 mm)	Pietsch, 1976	LACM 11235-25
	<i>Haplophryne</i>	<i>mollis</i>	62 mm	2 (12–15 mm)	Munk and Bertelsen, 1983	AMS I.21365-8 <sup>h</sup>
	<i>Haplophryne</i>	<i>mollis</i>	52.5 mm	2 (11.5–12 mm)	Bertelsen and Pietsch, 1983	AMS I.20071-1
	<i>Haplophryne</i>	<i>mollis</i>	46 mm	11 mm	Bertelsen and Pietsch, 1983	AMS I.20314-14
	<i>Haplophryne</i>	<i>mollis</i>	39 mm	12.5 mm	Bertelsen and Pietsch, 1983	AMS I.20315-9
	<i>Haplophryne</i>	<i>mollis</i>	48 mm	2 (10.5–12 mm)	Bertelsen and Pietsch, 1983	AMS I.21364-3
	<i>Haplophryne</i>	<i>mollis</i>	54 mm	6 (8.9–10.5 mm)	Stewart and Pietsch, 1998	NMNZ P.26070
	<i>Haplophryne</i>	<i>mollis</i>	58 mm	2 (11.6–14.2 mm)	Stewart and Pietsch, 1998	NMNZ P.24927
	<i>Haplophryne</i>	<i>mollis</i>	60 mm	11 mm	Stewart and Pietsch, 1998	NMNZ P.24164
	<i>Haplophryne</i>	<i>mollis</i>	159 mm	2 (9.8–10.8 mm)	Stewart and Pietsch, 1998	NMNZ P.21248
	<i>Haplophryne</i>	<i>mollis</i>	60 mm	14 mm	Unpublished	CSIRO H.3286-01
	<i>Haplophryne</i>	<i>mollis</i>	47 mm	13 mm	Unpublished	MCZ 59223
	<i>Haplophryne</i>	<i>mollis</i>	45 mm	12 mm	Unpublished	MNH 2003-2032
	<i>Haplophryne</i>	<i>mollis</i>	48 mm	12 mm	Unpublished	MNH 2004-0810
	<i>Haplophryne</i>	<i>mollis</i>	45 mm	13.6 mm	Unpublished	NMNZ P.8045
	<i>Haplophryne</i>	<i>mollis</i>	51 mm	11.6 mm	Unpublished	NMNZ P.35370
	<i>Haplophryne</i>	<i>mollis</i>	70 mm	2 (11.4–11.5 mm)	Unpublished	NMNZ P.36807
	<i>Haplophryne</i>	<i>mollis</i>	52 mm	2 (10–10.3 mm)	Unpublished	NMV A.5924
	<i>Haplophryne</i>	<i>mollis</i>	35 mm	2 (10.5–11.5 mm)	Unpublished	SOC <sup>g</sup>

Table 1. Continued

Family	Genus	Species	Female	Male(s)	Author and date	Catalog number
	<i>Linophryne</i>	<i>algibarbata</i>	182 mm	29 mm	Behrmann, 1974	IMB
	<i>Linophryne</i>	<i>algibarbata</i>	155 mm	23 mm	Jónsson and Pálsson, 1999	IINH
	<i>Linophryne</i>	<i>arborifera</i>	77 mm	15 mm	Bertelsen, 1980a	ISH 2736/71
	<i>Linophryne</i>	<i>argyresca</i>	61 mm	12 mm	Regan and Trewavas, 1932	ZMUC P92142
	<i>Linophryne</i>	<i>bicornis</i>	185 mm	30 mm	Behrmann, 1977	IMB
	<i>Linophryne</i>	<i>bicornis</i>	180 mm	18 mm	Bertelsen, 1982	IOAN
	<i>Linophryne</i>	<i>bicornis</i>	101 mm	19 mm	Moore et al., 2003	MCZ 138063
	<i>Linophryne</i>	<i>brevibarbata</i>	86 mm	13.6 mm	Maul, 1961	MMF 18214
	<i>Linophryne</i>	<i>brevibarbata</i>	100 mm	18.5 mm	Bertelsen, 1980a	BMNH 1995.1.18.4
	<i>Linophryne</i>	<i>coronata</i>	225 mm	Remnant	Ponomarenko, 1959	PINRO
	<i>Linophryne</i>	<i>coronata</i>	219 mm	26 mm	Bertelsen, 1976	MRIR <sup>c</sup>
	<i>Linophryne</i>	<i>coronata</i>	290 mm TL	?	Jónsson et al., 1986	MRIR <sup>c</sup>
	<i>Linophryne</i>	<i>coronata</i>	152 mm	18 mm	Unpublished	ICMB
	<i>Linophryne</i>	<i>densiramus</i>	68 mm	9.0 mm	Parin et al., 1977	IOAN
	<i>Linophryne</i>	<i>densiramus</i>	71 mm	17 mm	Anderson and Leslie, 2001	RUSI 54760
	<i>Linophryne</i>	<i>densiramus</i>	68 mm	13.5 mm	Unpublished	CSIRO H.3210-02
	<i>Linophryne</i>	<i>densiramus</i>	70 mm	17.5 mm	Unpublished	RUSI 63715
	<i>Linophryne</i>	<i>indica</i>	42 mm	9.5 mm	Bertelsen, 1978	LACM 36046-11
	<i>Linophryne</i>	<i>indica</i>	51 mm	14.5 mm	Bertelsen, 1981	SIO 70-306
	<i>Linophryne</i>	<i>lucifer</i>	230 mm	24 mm	Jónsson, 1967	MRIR <sup>c</sup>
	<i>Linophryne</i>	<i>lucifer</i>	190 mm	24.5 mm	Bertelsen, 1982	IOAN
	<i>Linophryne</i>	<i>lucifer</i>	190 mm TL	30 mm TL	Unpublished	MRIR
	<i>Linophryne</i>	<i>lucifer</i>	180 mm TL	40 mm TL	Unpublished	MRIR
	<i>Linophryne</i>	<i>lucifer</i>	174 mm	23.5 mm	Unpublished	ZMUC P922290
	<i>Linophryne</i>	<i>lucifer</i>	275 mm	29 mm	Unpublished	ZMUC P922443
	<i>Linophryne</i>	<i>macrodon</i>	91 mm	21.5 mm	Pietsch, 1976	UF 233292
	<i>Linophryne</i>	<i>maderensis</i>	105 mm	15 mm	Unpublished	ZMB 33308 <sup>g</sup>
	<i>Linophryne</i>	<i>trewavasae</i>	73.5 mm	10.7 mm	Bertelsen, 1978	LACM 36116-5
	<i>Linophryne</i>	sp.	?	?	Jónsson et al., 1986	MRIR <sup>c</sup>
	<i>Photocorynus</i>	<i>spiniceps</i>	46 mm	7.3 mm	Regan, 1925b	ZMUC P92134
	<i>Photocorynus</i>	<i>spiniceps</i>	50.5 mm	7.0 mm	Unpublished	ISH 1913/71
	<i>Photocorynus</i>	<i>spiniceps</i>	46 mm	6.2 mm	Unpublished	SIO 70-326
	<i>Photocorynus</i>	<i>spiniceps</i>	49 mm	6.5 mm	Unpublished	SIO 70-346

Records of the Melanocetidae represent temporary attachment, in which male and female tissues are not fused, while those of other families represent examples of permanent sexual parasitism in which fusion between male and female is evident

Specimens listed as *Ceratiis* sp. have lost the illicium and/or esca and therefore cannot be fully identified

<sup>a</sup> One of two males removed, sent to Copenhagen, and cataloged ZMUC

<sup>b</sup> With evidence of an additional male lost before capture

<sup>c</sup> Discarded (Gunnar Jónsson, personal communication, 19 April 2004)

<sup>d</sup> Stuffed and mounted

<sup>e</sup> Part of the late Tokiharu Abe's private collection, whereabouts unknown (Kazuo Sakamoto, personal communication, 7 June 2004)

<sup>f</sup> One of three males sacrificed by Regan and Trewavas (1932) for histological study

<sup>g</sup> Peter Herring collection, Southampton Oceanography Centre, Southampton, England

<sup>h</sup> With scar left behind by a third male apparently lost before capture; males sacrificed by Munk and Bertelsen (1983) for histological study

<sup>i</sup> Specimen not examined by me (Peter Bartsch, personal communication, 16 February 2005)

## Historical Perspective

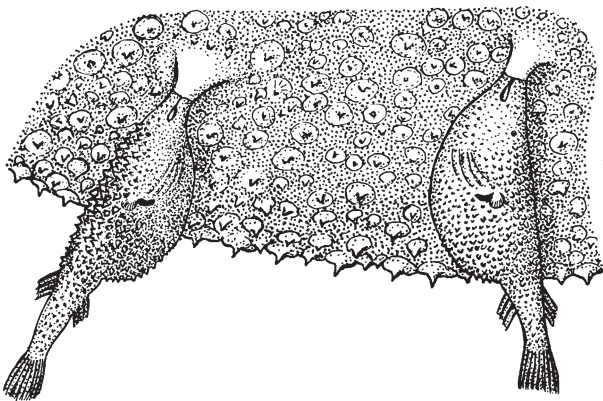
In 1922, the Icelandic fisheries biologist Bjarni Saemundsson (Fig. 2) published a remarkable description of two small fish attached by their snouts to the belly of a large female deep-sea anglerfish identified as *Ceratiis holboelli* (Fig. 3). Not recognizing them as males, Saemundsson (1922) described them as the young of the same species: "I can form no idea of how, or when, the larvae, or young, become attached to the mother; I cannot believe that the male fastens the egg to the female. This remains a puzzle for

some future researcher to solve" (Saemundsson, 1922: 164, translated from the Danish by H. Grönwold, in Regan, 1925b: 387–388). Three years later, Regan (1925a,b) dissected a small fish attached to a newly discovered female of *Ceratiis holboelli* and concluded that it must be a male parasitic on the female (Fig. 4). The male fish is "merely an appendage of the female, and entirely dependent on her for nutrition, . . . so perfect and complete is the union of husband and wife that one may almost be sure that their genital glands ripen simultaneously, and it is perhaps not too fanciful to think that the female may possibly be able to control

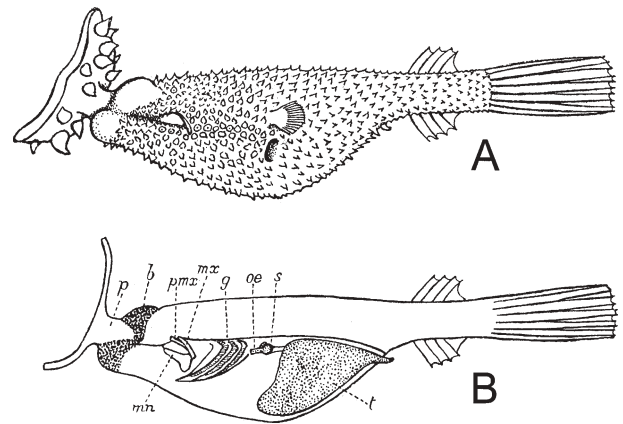




**Fig. 2.** Bjarni Saemundsson (1867–1940), Icelandic fisheries biologist and for 35 years (1905–1940) sole curator of what is now the Icelandic Institute of Natural History, Reykjavík (Courtesy of Steinunn Einarsdottir and Gunnar Jónsson)



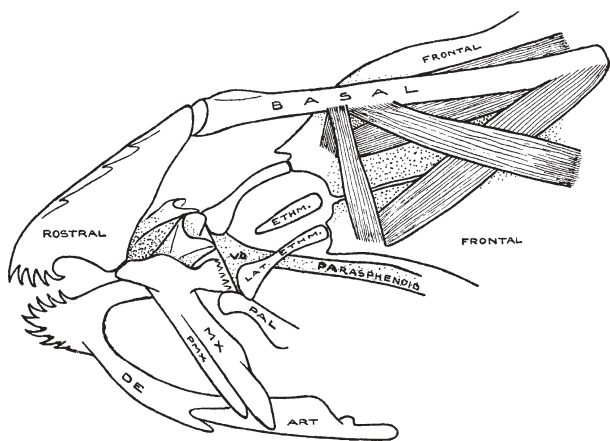
**Fig. 3.** Parasitic males of *Ceratias holboelli* attached to a 690-mm female; IINH (female and 60-mm male), ZMUC P922480 (second male, 65 mm). After Saemundsson (1922)



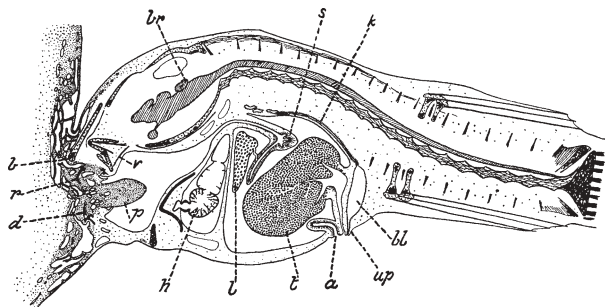
**Fig. 4.** Parasitic male of *Ceratias holboelli*, 75 mm, attached to a 670-mm female; BMNH 1924.12.29.2. **A** External view; **B** internal view; *b*, outgrowth of tissue at point of contact of male and female; *g*, gills; *mn*, mandible; *mx*, maxilla; *oe*, esophagus; *p*, papilla of female; *pmx*, premaxilla; *s*, stomach; *t*, testes. After Regan (1925b)

the seminal discharge of the male and to ensure that it takes place at the right time for fertilization of her eggs” (Regan, 1925b: 396–397).

Referring to them as “dwarfed males” that represented a heretofore unknown and “unique type of parasitism,” Regan (1925b: 397) searched for additional examples among the ceratioids collected by the Danish Dana Expedition of 1920–1922, discovering two additional attached males in the linophrynid genera *Photocorynus* and *Edriolychnus* (the latter now recognized as a junior synonym of *Haplophryne*). Finding this highly specialized reproductive mode in what were considered to be widely divergent taxa, Regan (1925b: 395) concluded that parasitic males are probably characteristic of all ceratioid fishes: “So far as is known . . . all the free-swimming ceratioids are females. Free-swimming males have not yet been found.” But shortly thereafter, Parr (1930b) found that the ceratioid family Aceratiidae, the contents of which were long thought to be taxonomically distinct from all other ceratioids because of their extremely small size and the absence of the luring apparatus, consisted entirely of free-living stages of males, heretofore recognized only in the attached form. Thus it became possible for the first time to assign the free-living males to the same genera and often to the same species as the females. In leading up to this discovery, Parr (1930a,b) was the first to show also that rostral structures found in the males are homologous to the bony support for the illicium of the females, and that these structures are primarily responsible for opening and closing the pincher-like denticular jaws that allow the males to grab and hold fast to the females (Fig. 5). Thus, assuming that males are at least partially attracted to the females by the bioluminescent display afforded by the illicium, the very structures that bring the sexes together are also those that allow for attachment. “An arrangement of this kind might certainly be regarded as an example of extreme phylogenetic economy of morphological parts” (Parr, 1930b: 134, fig. 6).



**Fig. 5.** Anatomy of the snout of a free-living male of *Melanocetus murrayi* (the holotype of *Rhynchoceratias longipinnis* Parr, 16mm, BOC 2592), showing how the basal bone (homologous to the pterygiophore of the illicium of females) controls movement of the rostral (upper denticular) bone, allowing the male to bite and hold fast to a female. ART, articular; DE, dentary; ETHM., ethmoid; LAT. ETHM., lateral ethmoid; MX, maxilla; PAL, palatine; PMX, premaxilla; VO, vomer. After Parr (1930a,b)



**Fig. 6.** One of three parasitic males of *Haplophryne mollis*, 12mm, attached to a 50-mm female (ZMUC P921777), composite sagittal section: a, anus; b, basal bone; bl, urinary bladder; br, brain; d, dentary; h, heart; k, kidney; l, liver; p, papilla of female tissue protruding into mouth of male; r, rostral denticle; s, stomach; t, testes; up, urinary papilla; v, vomer. After Regan and Trewavas (1932)

Parr (1930b) supposed further that all the free-living metamorphosed males that had previously been placed in the anomalous family Aceratiidae sooner or later become attached parasitically to females. However, in support of earlier assumptions made by Regan and Trewavas (1932: 21), Waterman (1939: 75) suggested that perhaps “in the more primitive families of the sub-order, in which no attached males have yet been found, that instead of actually growing fast to the females, . . . the males merely nip on to females for a relatively short period.” The supposition that a temporary attachment might occur in those species whose males do not become parasitic was further supported by Bertelsen (1951: 257), who found evidence that the males of some ceratioids never become parasitic: whereas free-living, metamorphosed males of families in which parasitic males

have been found become attached when immature and do not feed after metamorphosis, “free-living himantolophid males grow essentially after metamorphosis and, according to the contents of their stomachs, melanocetid males must also be able to feed at this stage. In these and also the families Oneirodidae and Gigantactinidae, the testes of the free-living males attain a very considerable size and it is most probable that males of these four families never become parasitic, but only attach themselves for a time to the female by means of their denticular apparatus.”

Bertelsen (1951: 250) found further that the males of those families that never become parasitic have an especially well-developed, toothed “denticular apparatus” (originating during metamorphosis by fusion of modified dermal spinules anterior to the toothed premaxillae and dentaries; see Munk, 2000) on the tips of the snout and chin that he believed must be used for “a temporary attachment to the female without subsequent fusion.”

The physiological aspects of the attachment of males to females in deep-sea anglerfishes have been only superficially explored. Regan (1925b, 1926) reported that longitudinal sections of tissue taken from the junction of an attached male and female *Ceratias holboelli* seemed to demonstrate a complete blending of tissues: “the highly vascularized fibrous tissue of the outgrowths of the male are continuous with that of . . . the female; in both, the general direction of the fibers and of the blood vessels is longitudinal, i.e., leading from one fish to the other, and it seems almost certain that the blood-systems of the two fishes are continuous and that the male is nourished by the female” (Regan, 1926: 12). Subsequent work by Regan and Trewavas (1932, see Fig. 6), Bertelsen (1951), Shoemaker (1958), Pietsch (1976), Munk and Bertelsen (1983), and Munk (2000) fully substantiated the earlier findings. “In the neighborhood of the fusion area the skin of the female is rendered spongy by the development of a system of thin-walled irregular intercommunicating blood-sinuses, which are continuous with similar sinuses in the skin and underlying tissues of the snout and jaws of the male” (Regan and Trewavas, 1932: 15). With this information, in addition to finding a poorly developed alimentary canal in the attached males, Regan (1925b, 1926) and Regan and Trewavas (1932) maintained that the attached males were nutritional parasites on the females. Furthermore, since all attached males known at the time retained lateral openings to the mouth just behind the area of attachment, and all males examined had a well-developed heart and gills, it was also concluded that “the male does not depend on the blood of the female for oxygen, but only for nutritive materials” (Regan 1926: 14). But, while Regan (1925b: 392) and others maintained that the vascular systems of both sexes unite, Waterman (1939: 77) suggested that nourishment of the male may be accomplished by a placenta-like arrangement of male-female tissues in the area of fusion, a notion that was accepted without evidence by Norman and Greenwood (1975: 274). That a placenta might exist was considered by Regan (1925b: 13), but he thought it “unlikely, for a placenta is essentially an attachment between two individuals that separate later on; but when the attachment is permanent

such a complication is unnecessary and need not be expected.”

By whatever means energy is acquired, Parr (1930b, 1932) suggested that the nutriment received by the males from the blood of the females may not be as important as originally suggested by Regan (1925b). “The enormous size of the liver [found in attached males], particularly in comparison with the greatly reduced alimentary canal, is, under the circumstances, much more easily understood in relation to the food storage properties of this organ than in relation to its digestive functions, and it may not be unreasonable to assume that its own liver, not the blood of the female, may be the most important factor in sustaining the life and further growth and maturing of the male after it becomes attached to a female” (Parr 1930b: 135). Parr (1930b, 1932) believed further that the relationship between male and female should not be thought of as a case of true parasitism but simply a protracted mating that may last a few months, at least not longer than the male is able to maintain itself on its own resources.

Bertelsen (1951), however, in opposition to Parr (1930b, 1932), presented considerable evidence to show that, at least in *Ceratias holboelli*: (1) attachment is probably of considerable duration; (2) males grow considerably after attachment, increasing their weight several hundred times; and (3) after metamorphosis, but before attachment, males do not increase in body weight, and the liver decreases somewhat in size during this period. These facts indicate that free-living metamorphosed males of this species do not eat on their own, but are sustained by the food stored in the liver, both in the free-living stage after metamorphosis and in the period from attachment until effective connection with the blood system of the female has been made. Finding no reason to doubt that attached males of other ceratioids are also nourished in the same manner as *Ceratias*, Bertelsen (1951: 245) concluded that “in all species and presumably in all families where attached males are found, the males are true parasites.”

Shoemaker (1958: 145) made histological sections through the region of attachment of one of three males attached to a female of *Cryptopsaras couesii* and concluded that the circulatory systems of the two were in fact fused: “It was quite clear that blood sinuses in this area communicated directly with blood vessels of both male and female.” Wickler (1961) described the structure and function of the angling apparatus of ceratioids and discussed some problems of pair formation. Pietsch and Nafpaktitis (1971) described an anomalous case of a sexually mature male of *Melanocetus johnsonii* (Melanocetidae) attached, but without tissue fusion, to an adolescent female *Centrophryne spinulosa* (Centrophrynidae). Olsson (1974) reexamined histological sections of an attached male of *Edriolychnus schmidti* (a junior synonym of *Haplophryne mollis*) described and figured by Regan and Trewavas (1932: 15–17, figs. 3–6), with respect to the endocrine glands. Results showed that those organs involved in regulation of various internal physiological factors, as well as those involved in adaptation to external factors, appear to be poorly developed or reduced, whereas mechanisms regulating reproduc-

tive activities seem to be well developed. Pietsch (1976) summarized what was known about sexual parasitism to date, describing male–female attachment in a number of previously unreported specimens and taxa, including several examples of surprisingly small parasitized females (for example, a 15.5-mm female of *Cryptopsaras couesii*, with a 9.8-mm attached male), but more importantly providing evidence that parasitism may be facultative in some ceratioids. Finally, Munk and Bertelsen (1983) provided the first detailed histological examination of parasitic attachment in a ceratioid, supporting the assumption that, at least in *Haplophryne mollis*, a connection is established between the vascular systems of male and female. This conclusion was reaffirmed by Munk (2000: 322), but he cautioned that, despite a high probability, there is as yet “no critical proof of a real continuity between the female blood vascular system and that of the parasitic male” in any ceratioid.

In summarizing his discovery of sexual parasitism in deep-sea anglerfishes, Regan (1926: 14) proposed the following scenario:

“The reason why the Ceratioids, alone amongst Vertebrates, have males of this kind is evident. They are necessarily few in numbers in comparison with the more active fishes on which they prey, and they lead a solitary life, floating about in the darkness of the middle depths of the ocean. Under such circumstances it would be very difficult for a mature fish to find a mate, but this difficulty appears to some extent to have been got over by the males, soon after they are hatched, when they are relatively numerous, attaching themselves to the females, if they are fortunate enough to meet them, and remaining attached throughout life. In all probability the males are incapable of free development, and it is likely that the great majority of them fail to find a female and perish, although another possibility has been suggested to me, namely, that the post-larval fish that find and become attached to females develop into males, and those that do not into females.”

The question of sex change in ceratioids was dispelled by Bertelsen (1951), who demonstrated for the first time that males and females of most species can be readily distinguished in the smallest larvae (2–3 mm in total length) by the early development of the illicial apparatus, appearing as a small undifferentiated papilla on the snout of females. Of 2366 larvae examined, the sex of only 142 (6%) was ranked as uncertain (Bertelsen, 1951: 248). Although these collections contain slightly more larval females than males, correcting for the type of gear used, and calculating on the basis of how many specimens of each sex would be caught if the fishing had been equally great at all depths, males amount to an average of 56% in areas around the world where ceratioids are most abundant. However, assuming that the females represent several year-groups and the free-living males only one, and considering further that females, with their self-advertising bioluminescence, are under greater predation pressure, Bertelsen (1951: 249) surmised that for



every female there are at least 15–30 metamorphosed males, the great majority of which would be mature or ready to attach themselves.

Bertelsen (1951), in a review of the literature and a worldwide search of collections, listed only 20 examples of females with parasitic males. In a similar survey made 25 years later, Pietsch (1976) raised the number to 45. Now, after another 25 years, the number has increased to 155 (Table 1). Most of these additional records are the result of a more intense search of preexisting collections, but a few are new and noteworthy. These are described below, along with information for each ceratioid family on taxonomic content, available material, occurrence of sexual parasitism, gravid females and ripe males, the development of eyes and nostrils of the males, the ability of males to capture and ingest food independently of the female, occurrences of multiple attachments of males to a single female, and the nature of the fusion between coupled males and females.

## Methods and Materials

Unless stated otherwise, standard length (SL) is used throughout; total length (TL) is used only when standard length is unknown. The illicium is the first dorsal-fin spine that bears the esca. The esca (or esca bulb, with esca appendages and filaments excluded) is the distal swelling of the illicium that contains the bacteria-mediated light organ (photophore). Definitions of terms used for the different states of development follow Bertelsen (1951: 10–11). “Fig.” is capitalized when referring to a figure reproduced herein, but presented in lower case when referring to figures found in literature cited.

Because ceratioids are still extremely rare and curators nearly always reluctant to sacrifice specimens, the developmental state of gonads has been subjected to little or no histological verification. Sexually mature or gravid individuals are assumed to be those whose gonads are obviously larger than those of other conspecific individuals of a similar standard length. Symbolic codes for institutions are those provided by Leviton et al. (1985), except for ASIZP (Academia Sinica, Institute of Zoology, Taipei, Taiwan), ECSFRI (East China Sea Fisheries Research Institute, Shanghai, China), HBOI (Harbor Branch Oceanographic Institution, Fort Pierce, Florida), ICMB (Instituto de Ciencias del Mar de Barcelona, Spain), IINH (Icelandic Institute of Natural History, Reykjavik, Iceland), IMB (Institut für Meeresforschung, Bremerhaven, Germany, now part of the Alfred Wegener Institut, Bremerhaven), INM (Ibaraki Nature Museum, Ibaraki, Japan); MNHNC (Station de Biologie Marine du Muséum National d’Histoire Naturelle et du Collège de France, Concarneau), MRIR (Marine Research Institute, Reykjavik, Iceland), MTF (Museum of Thorshavn, Faeroe Islands, Denmark), PINRO (Polar Research Institute of Marine Fisheries, Murmansk, Russia), and SOC (Southampton Oceanography Centre, Southampton, England). Specimens identified by institutional codes but without accompanying numbers are un-

cataloged. Pertinent material, not previously recorded in the literature, is listed as follows:

Caulophryniidae.—*Caulophryne jordani*: MRIR, 4 females (119–155 mm). *Caulophryne polynema*: MNHN 2001–0140, 137-mm female, with 15-mm parasitic male. *Caulophryne* sp.: MCZ 69324, 11-mm, free-living male in late metamorphosis.

Melanocetidae.—*Melanocetus johnsonii*: BMNH 2004.6.3.2–3, 75-mm female, with 23.5-mm male, attached, but without tissue fusion. *Melanocetus murrayi*: BSKU 57842, 73-mm female, with 15-mm male, attached, but without tissue fusion.

Himantolophidae.—*Himantolophus breviostris*-group: BMNH 2004.6.29.13, male, 30 mm; BMNH 1969.6.26.3291, male, 31 mm; BMNH 2004.9.12.141, male, 35 mm. *Himantolophus rostratus*-group: UF 232657, largest known male, 39 mm. *Himantolophus* sp.: BMNH 2004.9.12.143–144, 2 males, 31.5–33 mm; BMNH 2004.11.6.32, male, 32 mm; BMNH 2004.11.6.118, male, 36 mm; MNHN 2004-1791, male, 30 mm; MNHN 2004-1846, male, 36 mm.

Diceratiidae.—*Bufoceratias thele*: ASIZP 65075, female, 200 mm, large ovaries containing immature eggs. *Diceratias pileatus*: UF 233052, female, 235 mm; BPBM 30655, female, 275 mm, both with large ovaries.

Oneirodidae.—*Bertella idiomorpha*: OSUO 1045, female, 84 mm; SIO 92-175, female, 101 mm; UW 48712, 77-mm female, with 11-mm parasitic male. *Leptacanthichthys gracilispinis*: LACM 33625-2, 56-mm female, with 7.5-mm parasitic male.

Thaumatichthyidae.—*Lasiognathus amphirhamphus*: BMNH 2003.11.16.12, female, 157 mm. *Thaumatichthys axeli*: ZMUC P92166, female, 365 mm. *Thaumatichthys binghami*: TCWC 6338.08, female, 62.5 mm; TCWC 10922.09, female, 130 mm; UW 47537, female, 83 mm; USNM 21471, female, 294 mm; UW 47130, larval male, 15 mm; UW 47520, free-living adolescent male, 36 mm; ZMUC P921946, free-living adolescent male, 31 mm. *Thaumatichthys* sp.: ASIZP 63971, female, 246 mm.

Centrophryniidae.—*Centrophryne spinulosa*: ASIZP 59902, female, 247 mm, largest known specimen.

Ceratiidae.—*Ceratias holboelli*: HUMZ 95300, 690-mm female, with 105-mm parasitic male; MRIR, 4 females (900–1210 mm TL), each with a parasitic male (70–190 mm TL). *Ceratias* sp.: CAS 60358, 370-mm female, with 5-mm remnant of a parasitic male; CAS 82498, female not preserved, patch of skin with 73-mm parasitic male; LACM 36955-1, 275-mm female, with 24.5-mm parasitic male; MNHN 2004-1518, 660-mm female, with 46-mm parasitic male; MTF, 740-mm female, with 60-mm parasitic males; UW 22322, 553-mm female, with 46-mm parasitic male; ZMH 21014, 750-mm female, with 115-mm parasitic male. *Cryptopsaras couesii*: ARC 8707665, 45-mm female, with 10-mm parasitic male; CAS 73320, 215-mm female, with 44-mm parasitic male; CAS 76509, 195-mm female, with 34-mm parasitic male; HUMZ 69165, 324-mm female, with 48-mm parasitic male; HUMZ 69166, 345-mm female, with 6 (18–44 mm) parasitic males; HUMZ 73014, 308-mm female, with 4 (78–88 mm) parasitic males; HUMZ 98265, 320-mm female, with 48-mm parasitic male; MCZ 164112, 162-mm female, with 24.5-mm parasitic male; NMNZ P.34960, 390-mm female, with 2 (47–99 mm) parasitic males; OSUO 12056, 252-mm female, with 62-mm parasitic male; SIO 95-30, 302-mm female, with 50-mm parasitic male; SIO 97-52, 202-mm female, with 20-mm parasitic male; UF 25157, 94-mm female, with 2 (8–14.5 mm) parasitic males; UF 25160, 164.5-mm female, with 49-mm parasitic male; UF 25164, 108-mm female, with 20.5-mm parasitic male; USNM 219906, 132-mm female, with 17-mm parasitic male; UW 21774, 215-mm female, with 20-mm parasitic male; UW 21775, 240-mm female, with 34-mm parasitic male; UW 46112, 230-mm female, with 80-mm parasitic male.

Gigantactinidae.—*Rhynchactis macrothrix*: ASIZP 61797, female, 136 mm, with large ovaries; ASIZP 62880, female, 70 mm.

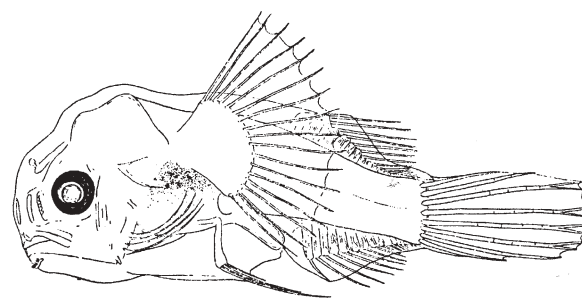
Neoceratiidae.—*Neoceratias spinifer*: LACM 32797-3, female, 23.5 mm; MCZ 51292, 17-mm female; MCZ 61075, female, 21 mm; SIO 56-133, female, 33 mm; SIO 68-476, female, 46.5 mm; SIO 68-478, 3 females, 17–67.5 mm, 67.5-mm specimen, with 17.5-mm parasitic male; SIO 70-306, female, 17 mm.

Linophryinae.—*Acentrophryne longidens*: HUMZ 167353, female, 56 mm; HUMZ 175257, female, 110 mm; HUMZ 189134, female, 51 mm. *Borophryne apogon*: USNM 326570, 65.5-mm female, with 12-mm parasitic male. *Haplophryne mollis*: MCZ 59223, 47-mm female, with 13-mm parasitic male; MNHN 2003-2032, 45-mm female, with 12-mm parasitic male; MNHN 2004-0810, 48-mm female, with 12-mm parasitic male; NMNZ P.8045, 44-mm female, with 13.6-mm parasitic male; NMNZ P.35370, 51-mm female, with 11.6-mm parasitic male; NMNZ P.36807, 70-mm female, with 2 (11.4–11.5 mm) parasitic males; NMV A.5924, 52-mm female, with 2 (10–10.3 mm) parasitic males; SOC, 35-mm female, with 2 (10.5–11.5 mm) parasitic males. *Linophryne densiramus*: RUSI 63715, 70-mm female, with 17.5-mm parasitic male. *Linophryne lucifer*: MRIR, 190-mm TL female, with 30-mm TL male; MRIR, 180-mm TL female, with 40-mm TL parasitic male; ZMUC P922290, 174-mm female, with 23.5-mm parasitic male; ZMUC P922443, 275-mm female, with 29-mm parasitic male; *Linophryne maderensis*: ZMB 33308, 105-mm female, with 15-mm parasitic male. *Photocorynus spiniceps*: ISH 1913/71, 50.5-mm female, with 7-mm parasitic male; SIO 70-326, 46-mm female, with 6.2-mm parasitic male; SIO 70-346, 49-mm female, with 6.5-mm parasitic male; all males with ripe testes.

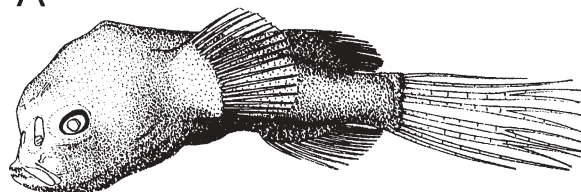
## Family Accounts

**Caulophrynidae.** The family Caulophrynidae, now containing two genera (*Caulophryne* Goode and Bean, 1896; and *Robia* Pietsch, 1979) and five species, is currently represented in collections by some 60 females, five males, and 16 larvae (Bertelsen, 1951; Pietsch, 1979). Two of the males are free-living: a 7.5-mm specimen in an early stage of metamorphosis (ZMUC P92193, Fig. 7A) and an 11-mm specimen in late metamorphosis (MCZ 69324, Fig. 7B). The remaining three are parasitically attached to females (see Table 1). Two of the latter are assigned to *Caulophryne polynema*: the holotype of the species, a 16-mm male attached to a 142-mm female (BMNH 1930.2.7.1) described in detail by Regan (1930b); and a previously unrecorded pair, a 15-mm male attached to a 137-mm female (MNHN 2001-0140, Fig. 8A). The third known example of sexual parasitism in caulophrynids is a 12-mm male attached to a 98-mm female (LACM 36025-1, Fig. 9A) identified by Pietsch (1979) as *Caulophryne* sp.

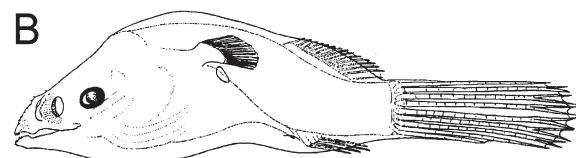
The gonads of the BMNH pair have not been examined directly, but the “abdomen [of the male] is somewhat swollen, no doubt by the developing testes” (Regan, 1930b: 194, fig. 3). Those of the LACM pair are large in each case: the right ovary of the female is 22 mm long (22.4% SL) and contains numerous eggs approximately 0.3 mm in diameter; the testes of the male are 2.3 mm long (19.2% SL). Unfortunately, the male attached to MNHN 2001-0140 has been eviscerated, perhaps by damage upon capture, but more likely by later dissection. The length of the ovaries of the



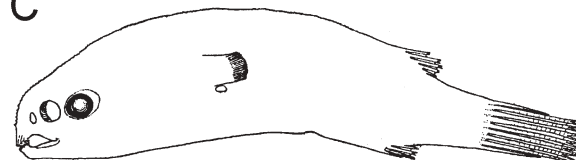
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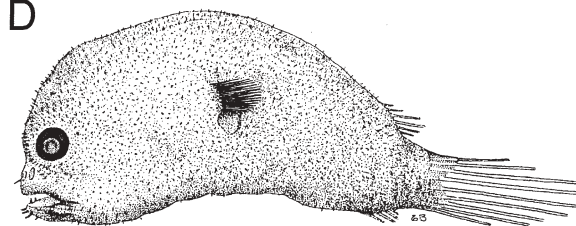
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C



D

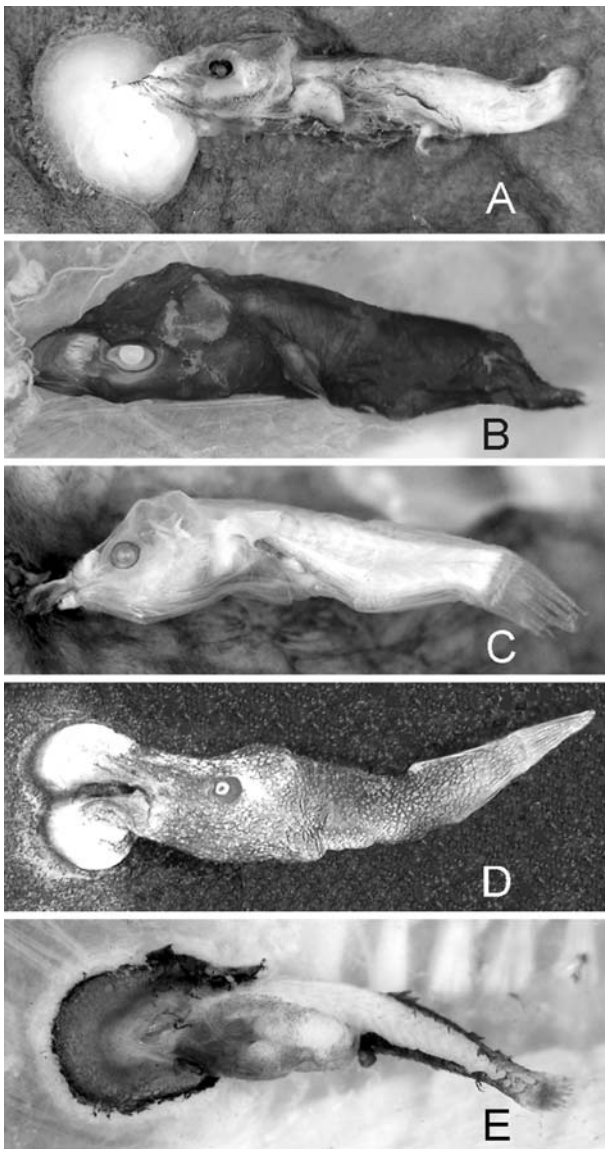


E

**Fig. 7.** Free-living males. **A** *Caulophryne* sp., 7.5 mm, ZMUC P92193, in late metamorphosis, showing presence of pelvic fins; **B** *Caulophryne* sp., 11 mm, MCZ 69324, in late metamorphosis; **C** *Melanocetus* sp., 20 mm, ZMUC P92458; **D** *Himantolophus* sp., 34.5 mm, ZMUC P92675; **E** Diceratiidae, 14 mm, LACM 36091-4. After Bertelsen (1951, 1983)

female is about 23% SL, each containing thousands of tiny eggs, approximately 0.15–0.20 mm in diameter.

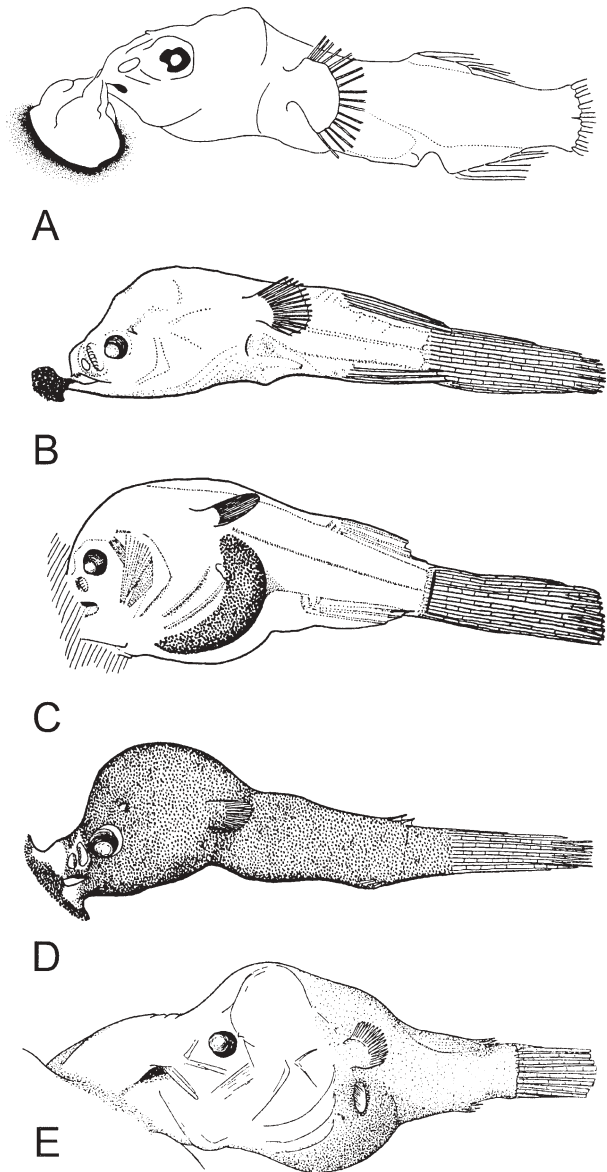
The ovaries of a number of large nonparasitized females of *Caulophryne jordani* are well developed, indicating that females may become sexually mature in the absence of a male: the length of those of a 109-mm specimen from off Newfoundland (ROM 27250) are nearly 30% SL and filled with numerous eggs measuring approximately 0.2 mm in diameter (Pietsch, 1976); lengths of those of four specimens from off Iceland (MRIR) are 16.8% SL in a 119-mm specimen, 26.9% SL in a 130-mm specimen, 27.4% SL in



**Fig. 8.** Parasitic and temporarily attached males. **A** *Caulophryne polynema*, 15 mm, parasitically attached to a 137-mm female, MNHN 2001-140; **B** *Melanocetus murrayi*, 15 mm, temporarily attached (without tissue fusion) to a 73-mm female, BSKU 57842; **C** *Bertella idiomorpha*, 11 mm, parasitically attached to a 77-mm female, UW 48712; **D** *Cryptopsaras couesii*, 10 mm, parasitically attached to a 45-mm female, ARC 8707665; **E** *Neoceratias spinifer*, 18 mm, parasitically attached to a 108-mm female, SIO 70-336

a 153-mm specimen (containing thousands of tiny eggs), and 22.3% SL in a 155-mm specimen. The testes of the two known free-living males are small and apparently immature.

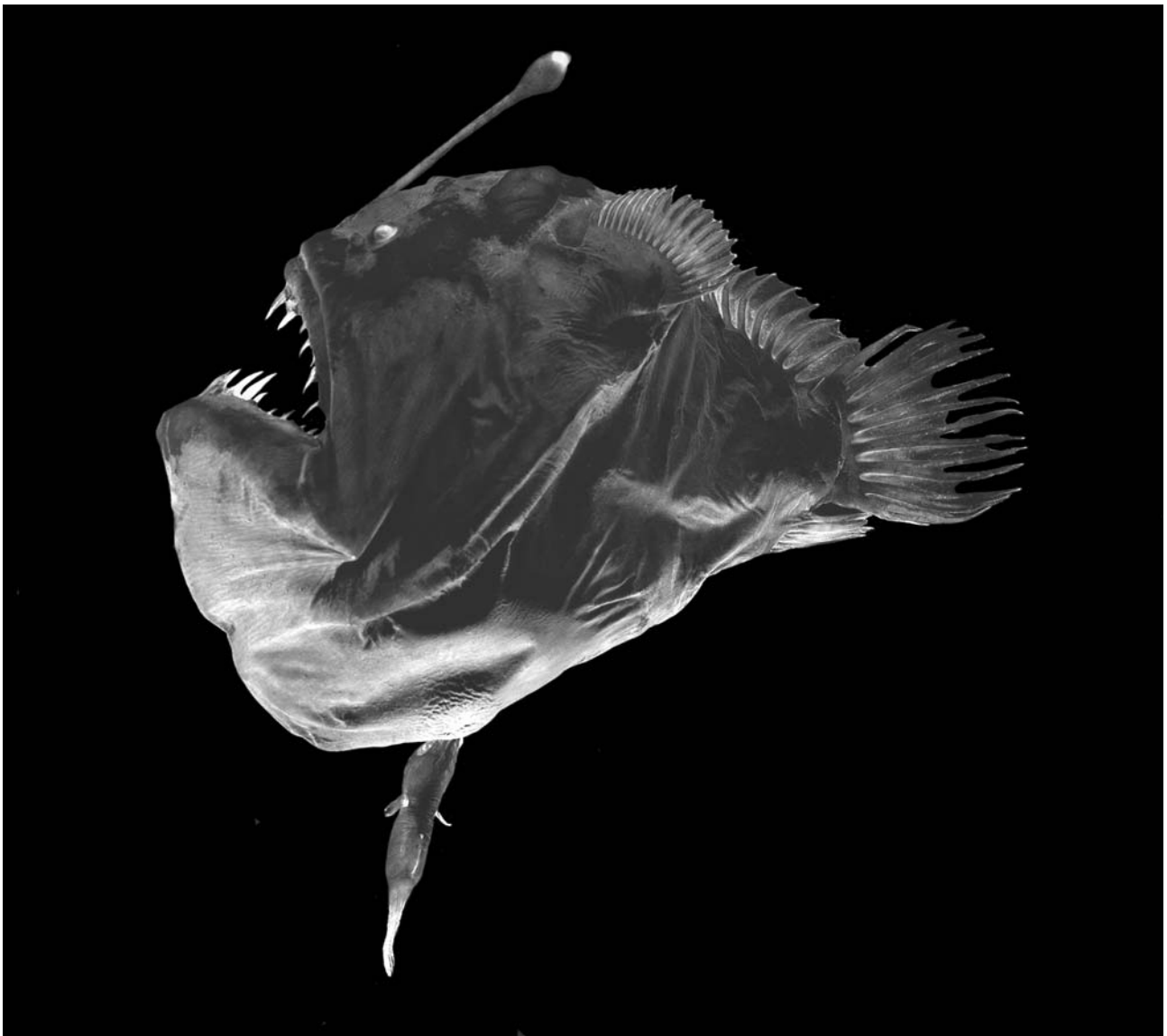
In all three known cases of sexual parasitism, the male is joined to the female on the belly (just slightly to the left or right of the midline and facing forward in the same direction as the female as if the male approached the female from behind) by means of separate outgrowths of tissue from the snout and lower jaw that unite with the distal surface of a prominent, unpigmented, conical or hemispherical out-



**Fig. 9.** Parasitic males. **A** *Caulophryne* sp., 12 mm, attached to a 98-mm female, LACM 36025-1 (after Pietsch, 1979); **B** *Borophryne apogon*, 14.5 mm, attached to a 47-mm female, BMNH 1932.5.3.38 (after Regan and Trewavas, 1932); **C** *Haplophryne mollis*, 12 mm, one of three attached to a 50-mm female, ZMUC P921777 (after Regan and Trewavas, 1932); **D** *Linophryne argyresca*, 12 mm, attached to a 61-mm female, ZMUC P92142 (after Regan and Trewavas, 1932); **E** *Photocorynus spiniceps*, 7.4 mm, attached to a 46-mm female, ZMUC P92133 (after Bertelsen, 1951)

growth from the female (diameter nearly 5% SL in the 137-mm female; see Pietsch, 1979: 20, fig. 23; Figs. 8A, 9A). Thus, the heads of the males are neither embedded in, nor broadly attached to, the surface of the female, but rather a considerable distance is maintained between the two by newly formed tissue. The males are upside down relative to the females in the BMNH and LACM specimens, but right-side up in the MNHN specimen. In all three examples, prominent openings to the mouth and opercular cavities are re-





**Fig. 10.** *Melanocetus johnsonii*, 75-mm female, with a 23.5-mm attached male, BMNH 2004.6.3.2-3. (Photograph by Edith A. Widder)

tained on both sides, and there is no papilla of female tissue extending into the mouth of the male, characteristic of couplings in some other taxa (for example, *Haplophryne*; see below). A comparison of all three attached males shows no significant morphological differences. Relative to other ceratioid males, those of caulophrynids have large eyes, with a conspicuous aphakic space anterior to the lens; the olfactory organs are also large, at least in free-living stages, but appear to degenerate quickly upon attachment to a female. For more details, see Regan (1930b) and Pietsch (1976, 1979).

**Melanocetidae.** The Melanocetidae, containing a single genus (*Melanocetus* Günther, 1864) and six species (Pietsch and Van Duzer, 1980), is now known from more than 800 females, at least 120 free-living males, and about 400 larvae. Until very recently, the only evidence of sexual parasitism in this family was an anomalous case of a 20-mm male

*Melanocetus johnsonii* attached to the upper lip of a 168-mm female *Centrophryne spinulosa* (LACM 30843-1; Pietsch and Nafpaktitis, 1971; see Centrophrynidae, below). However, the attachment did not involve fusion of male-female tissue and is therefore not considered to be a parasitic association. Two similar couplings in *Melanocetus*, but between sexes of the same taxon, have recently been discovered. One of these, a 23.5-mm male attached to a 75-mm female *Melanocetus johnsonii* (BMNH 2004.6.3.2-3, Fig. 10), was collected in the eastern North Atlantic off Ireland in 1999 by the RRS *Discovery* in a cruise partially funded by the British Broadcasting Corporation for the celebrated “Blue Planet” video series. The second example is part of collections made by Hiromitsu Endo, aboard the R/V *Tansei-Maru*, west of Okinawa, in April 2002: a 15-mm male attached to a 73-mm female *Melanocetus murrayi* (BSKU 57842, Fig. 8B). Both males are only loosely attached, with



tissue of the female pinched by the tightly closed denticular jaws of the male, the BMNH example hanging from the middle of the belly of the female, and the BSKU specimen attached to the right side of the head of the female, just beneath the sphenotic bone. In both cases, it does not appear that any fusion of male and female tissue has taken place. Either the connections of the two were so recent that the tissues did not have time to fuse, or, more likely, these are the first and only known examples of a nonparasitic coupling—male ceratioids caught in the act of temporary attachment.

The gonads of the smaller of the two melanocetid couples are not especially large: the testes are only about 1.9 mm long (12.7% SL), but histological examination shows them to be at an early stage of resorption (therefore indicating a recent spawning event), with a small number of sperm heads evident; the ovaries are about 12 mm long (16.4% SL) and contain thousands of tiny eggs, each approximately 0.20–0.25 mm in diameter. The testes of the larger pair are slightly smaller relative to standard length, about 2.7 mm long (11.5% SL), but histological examination shows numerous mature spermatozoa; the ovaries are huge, about 35 mm long (46.7% SL), containing thousands of slightly dehydrated eggs that are among the largest ever recorded for a ceratioid, each approximately 0.7–0.8 mm in diameter.

Metamorphosed free-living males of *Melanocetus* with large ripe testes have been described (Pietsch, 1976: 783), but personal examination of the ovaries of numerous females, including the largest known individuals of the family (up to 135 mm), failed to identify any females with eggs greater than about 0.10 mm in diameter (examination of more than 60 females recently collected from off Taiwan produced the same result; Hsuan-Ching Ho, personal communication, 25 August 2003). Metamorphosed males continue to feed after metamorphosis: food items have been found in their stomachs and considerable growth continues after stores in the liver have become exhausted (Bertelsen, 1951; Pietsch, 1976). This ability to take prey after metamorphosis is indicated by the relatively large, heavily toothed upper and lower denticular bones of adult *Melanocetus* males (Bertelsen, 1951: 39, 250; Pietsch, 1976: 783, fig. 1A). The eyes and nostrils of the males are large and well developed (Bertelsen, 1951: 48, fig. 16, 17, 19–21; see Fig. 7C). For more details on reproduction in melanocetids, see Pietsch (1976).

**Himantolophidae.** The family Himantolophidae, containing a single genus (*Himantolophus* Reinhardt, 1837) and 18 species distributed among five species-groups, is represented in collections around the world by more than 150 females, 48 free-living males, and 311 larvae (Bertelsen and Krefft, 1988). Except for the presence of white circular scars found on the bodies of 5 females, which Maul (1961: 115, fig. 15) argued might be “the result of an injury caused by a male that had grown fast there and has for some reason become suddenly detached,” but which Bertelsen and Krefft (1988) suggested might be caused by parasitic copepods, there is no evidence of sexual parasitism in this family.

Contrary to reports of ovaries containing ripe or nearly ripe eggs in a number of large females (Regan and Trewavas, 1932; Bertelsen, 1951; Mead et al., 1964), Bertelsen and Krefft (1988), based on a detailed examination of all known material, stated that “no fully mature females have been found.” Eggs with diameters of more than 0.10 mm were found in only four specimens (112–180 mm SL) and only one of these (145 mm SL) appeared to be near maturity. In the remaining larger females examined (90–328 mm SL), egg diameters varied between 0.05 and 0.10 mm and ovaries measured 9–31% SL in length and 6–13% SL in width. All smaller females examined (40–80 mm) had immature ovaries less than 10% SL in length and 5% SL in width. That several large females of *H. groenlandicus* from far northern Atlantic waters have spent ovaries (Saemundsson, 1927: 168; Bertelsen, 1951: 26) also appears to be unfounded. Those of several large specimens (185–328 mm), all caught in northern latitudes and assumed to be expatriates (but see Jónsson and Pálsson, 1999: 205), are somewhat enlarged (length 17–30% SL) but compressed (less than about 3% SL in width), containing only minute eggs in early developmental stages (Bertelsen and Krefft, 1988).

Contrary to the development of known females, numerous free-living himantolophid males have large well-developed testes (Regan and Trewavas, 1932; Bertelsen, 1951; Mead et al., 1964). As described by Bertelsen (1951), the testes show a distinct increase in relative size during late larval stages, become well developed in metamorphic stages, and nearly fill the body cavity in metamorphosed specimens. Those of three specimens (30.5–34 mm SL) examined microscopically by Bertelsen and Krefft (1988: 78) were filled with mature spermatozoa with elongate condensed nuclei and distinct tails. None of the known males appeared to be spent.

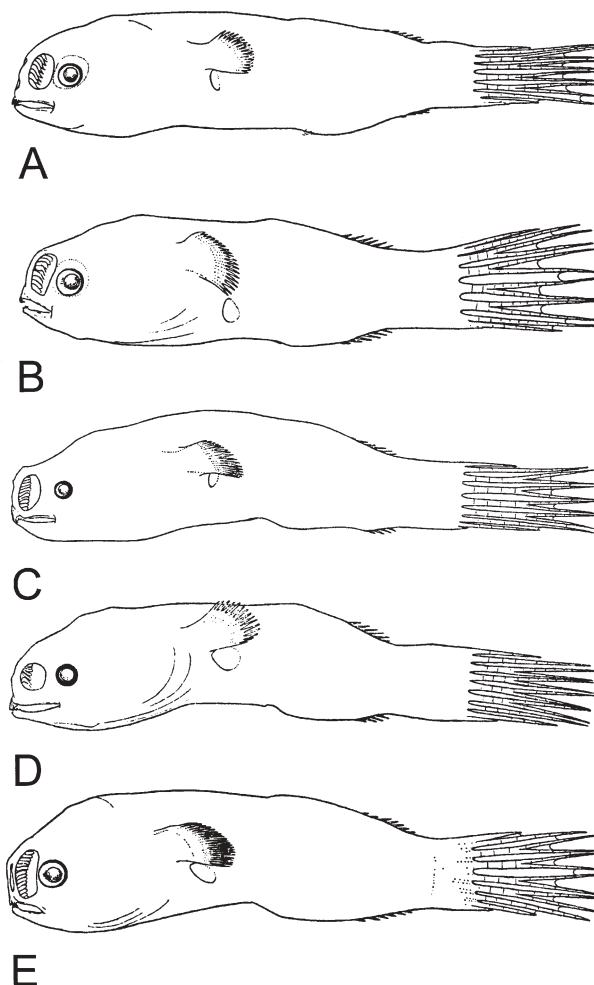
Similar to that of melanocetids and ceratiids, as described by Parr (1930b) and Bertelsen (1951), the denticular jaw apparatus of himantolophid males appears well adapted for nipping the skin of the females. It also seems well adapted for predation (Bertelsen and Krefft, 1988: 26, fig. 10), supporting the contention of Bertelsen (1951) that males of this family are able to feed on their own beyond metamorphosis. However, the latter assumption was not supported by the more detailed review of Bertelsen and Krefft (1988: 30), who found no evidence of continued postmetamorphic feeding of the males; even the existence of any post-metamorphic growth appears questionable. Of 38 metamorphosed males examined by them, the stomachs of 30 were distinctly reduced in size, their walls thin and transparent, and completely empty. Of the remaining 7 specimens, the stomachs of 2 (27–32 mm SL) contained an unidentifiable white substance (very similar to material found in the stomachs of a number of smaller metamorphosing males) and 1 of these 2 also contained the remains of chaetognath setae. Although this may be evidence of postmetamorphic feeding, it seems more likely that the observed food remains in the stomachs of these specimens originated from a last feeding in epi- or upper mesopelagic layers before full metamorphosis and descent into deeper waters where they

were captured. Thus, Bertelsen and Krefft (1988: 30) were unable to provide convincing proof that metamorphosed himantolophid males are able to eat on their own: "the possibility cannot be excluded that the store of nutrients in the liver and other tissues of the metamorphic males might be sufficient for the change in body proportions and the final development of the testes during and after metamorphosis."

Himantolophid males reach a greater adult size than free-living males of any other known ceratioid, the largest among the approximately 38 known metamorphosed specimens measuring 39 mm SL (UF 232657; Bertelsen and Krefft, 1988: 78, fig. 36). The olfactory organs are as well developed as those of most other ceratioid males, increasing significantly in relative size during metamorphosis, but the eyes are relatively small, actually decreasing slightly in relative diameter with increasing standard length (Fig. 7D). Contrary to the general assumption that pair formation in ceratioids is mediated at least in part by vision (Munk, 1966), the relatively small eyes of himantolophid males may not be capable of assisting in mate location and recognition (Bertelsen and Krefft, 1988: 26, 34). For more on reproduction in himantolophids, see Bertelsen and Krefft (1988).

**Diceratiidae.** The Diceratiidae, containing two genera (*Diceratias* Günther, 1887; and *Bufoceratias* Whitley, 1931) and six species, is now known on the basis of at least 100 females, a single metamorphosed free-living male, and two larvae (Uwate, 1979; Balushkin and Fedorov, 1986; Pietsch et al., 2004). Although still very poorly known, there is no evidence of sexual parasitism in this family (Pietsch, 1976; Bertelsen, 1983). The only known sexually mature diceratiid is a 235-mm female of *Diceratias pileatus* (UF 233052), the ovaries of which each contain  $10^4$  to  $10^5$  pear-shaped eggs, measuring 0.3–0.7 mm in diameter (Uwate, 1979). The ovaries of the largest known specimen of the family, a 275-mm female of *D. pileatus* (BPBM 30655), are large, their length approximately 80 mm or 29% SL, but they contain no eggs and appear to be spent (Pietsch and Randall, 1987). The ovaries of the largest known specimen of *Bufoceratias thele* (200 mm, ASIZP 65075) contain numerous developing eggs, 0.16–0.28 mm in diameter (Hsuan-Ching Ho, personal communication, 5 May 2004). Judging by the small olfactory organs and testes, the position and small size of the denticular teeth, and the retention of a few tiny larval teeth, the single known male (14 mm, LACM 36091-4) is a juvenile (Bertelsen, 1983: 312, fig. 1; Fig. 7E). The eyes are relatively well developed, measuring 1.2 mm in diameter (8.6% SL), each with a narrow aphakic space surrounding the lens.

**Oneirodidae.** The Oneirodidae is by far the largest, most complex, and certainly the least understood family of the suborder. With 16 genera and 62 species, it contains 40% of all recognized ceratioids. Of the 16 genera, 5 are currently represented by only one, two, or three adolescent or adult females; only 8 are represented by more than a dozen females. Males have been described for only 7 genera, while larvae are known for only 8. Despite the rareness of most recognized taxa, however, new oneirodids continue to be

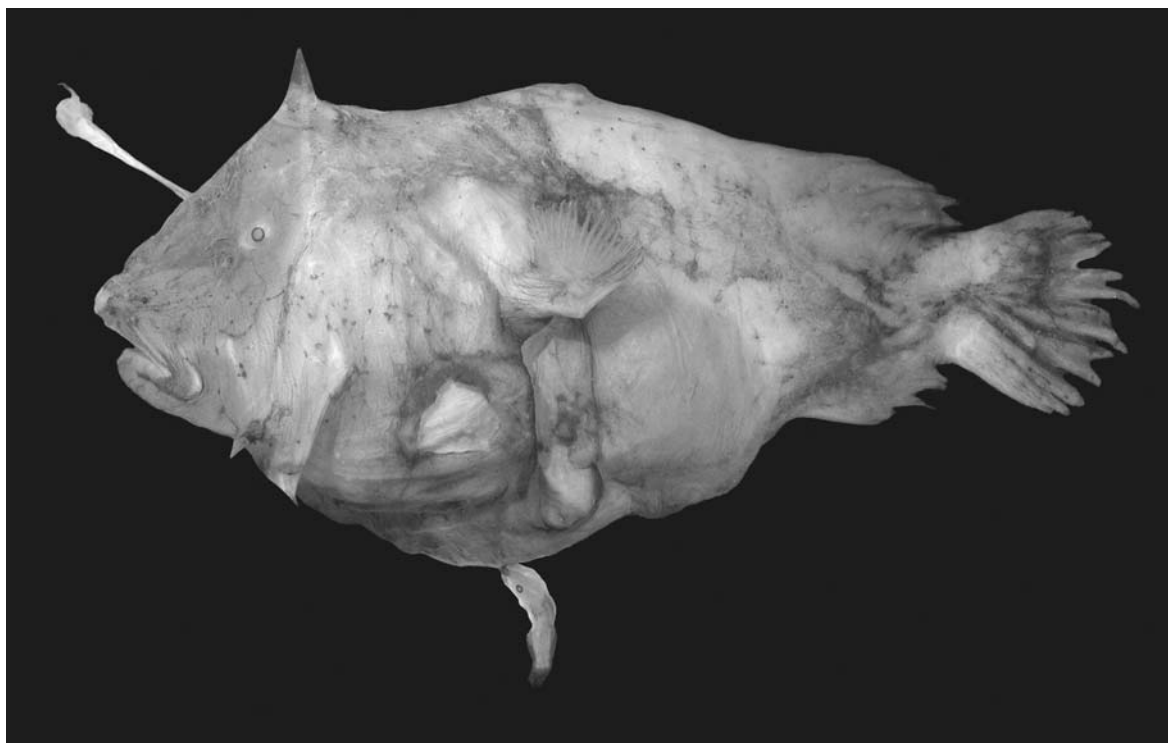


**Fig. 11.** Free-living males of oneirodids. **A** *Chaenophryne draco*-group, 14 mm, ZMUC P92686; **B** *Dolopichthys* sp., 12.5 mm, ZMUC P92799; **C** *Microlophichthys andracanthus*, 16.5 mm, ZMUC P9293; **D** *Oneirodes* sp., 12.5 mm, ZMUC P921016; **E** *Pentherichthys* sp., 13 mm, ZMUC P921113. (All after Bertelsen, 1951)

discovered (for example, Orr, 1991; Stewart and Pietsch, 1998; Ho and Shao, 2004; Pietsch, 2004).

The known material of the family has increased dramatically in the last quarter of a century. There are now at least 1200 females, about 164 free-living males, and 697 larvae in collections around the world. Among this material are 2 attached males, both representing the only known males of their respective genus and species: a 7.5-mm male attached to a 56-mm female of *Leptacanthichthys gracilispinis* (LACM 33625-2) described by Pietsch (1976: 784, figs. 2–5; 1978: 19, fig. 16) and a previously unreported, 11-mm male attached to a 77-mm female of *Bertella idiomorpha* (see below).

Before the discovery of these two attached males, there was no evidence to conclude that males of oneirodids ever become sexually parasitic. Food items have not been found in the stomach of any oneirodid male but, nevertheless, the males of at least some genera grow considerably after metamorphosis. For example, metamorphosis stages of



**Fig. 12.** *Bertella idiomorpha*, 77-mm female, with an 11-mm parasitic male, UW 48712

*Oneirodes* measure 6.0–9.5 mm, whereas the largest known metamorphosed specimen is 16.5 mm long (Pietsch, 1974, 1976). These data indicate that oneirodid males, all equipped with large, well-developed eyes and nostrils (Fig. 11), probably continue to feed after metamorphosis and are thus not nutritionally dependent on a parasitic association with the female. The especially well-developed denticular apparatus of males of this family has been thought to be used for temporary attachment without subsequent tissue fusion. The discovery of parasitized female oneirodids is therefore surprising and of considerable interest.

Except for a few details, the circumstances surrounding the attached male of *Bertella idiomorpha* (Figs. 8C, 12) are very similar to those described by Pietsch (1976, 1978) for that of *Leptacanthichthys gracilispinis*. Both are connected by a narrow cylindrical stalk of tissue protruding from the mid-belly of the female. The length of the stalk of *Bertella* is considerably less than that of *Leptacanthichthys*: 16 mm (2.1% SL) and 2.2 mm (3.9% SL), respectively. Whereas only the tip of the upper jaw of the male of *Leptacanthichthys* was embedded in the stalk of female tissue (since torn away, but the bones of the upper jaw and ethmoid region remain attached to the female; Pietsch, 1976: 784, fig. 2), the tips of both upper and lower jaws are fused with female tissue in *Bertella*. In the latter, small openings to the mouth and opercular cavities of the male are retained on both sides; in both couplings, there is no papilla of female tissue extending into the mouth of the male.

The male of *Leptacanthichthys*, at 7.5 mm, is in late metamorphosis, with subdermal pigment well developed and

skin only lightly pigmented (Pietsch, 1976: 785, fig. 4). The somewhat larger male of *Bertella*, at 11 mm, appears to be slightly more mature, lacking any visible subdermal pigment, but the dermal and subdermal pigmentation overall of both male and female has largely disappeared as a result of photochemical bleaching over time. Adolescent and adult males of most all known ceratioids are greater than approximately 10 mm SL (exceptions to this general rule are found primarily in the family Linophryniidae; see below), their subdermal pigmentation has disappeared, and the skin is darkly pigmented in all known genera except *Haplophryne* (see Bertelsen, 1951: 10, 167, fig. 112A).

The viscera of the two oneirodid males are similar (Pietsch, 1976: 785, fig. 5), each having a moderately sized liver occupying a third or less of the volume of the coelomic cavity. The paired testes are small (their length 0.9 mm or only about 8.2% SL in *Bertella*) compared to those of a ripe male (greater than 20% SL and filling most of the abdominal cavity in some specimens; for example, see Jespersen, 1984). Serial sections through the entire length of both testes of the *Leptacanthichthys* male revealed only small undifferentiated spermatocytes. In contrast, the gonads of both females are well developed. The left ovary of *Leptacanthichthys* is filled with approximately 7500 eggs, measuring approximately 0.4–0.6 mm in diameter, and those of *Bertella* contain a similar number of slightly larger eggs (among the largest known for any ceratioid), approximately 0.6–0.8 mm in diameter (but now somewhat dehydrated; the eggs were undoubtedly larger in life).

Several facts indicate that these two couplings represent permanent parasitic associations of male and female rather



than temporary attachments: (1) definite evidence of tissue fusion between male and female exists in both cases; (2) although not examined histologically in *Bertella*, the stalk of female tissue of *Leptacanthichthys*, to which the male was attached, is full of intercommunicating vessels (Pietsch, 1976: 785, fig. 3) capable of transferring blood and nutrients to the male (much like those described in the area of fusion of parasitic males of other ceratioids; see Regan and Trewavas, 1932, figs. 4, 5; Munk and Bertelsen, 1983, figs. 4–12); and (3) as shown by their small size, unpigmented skin, and undeveloped testes, the males are sexually immature; metamorphosed males of ceratioid families that exhibit sexual parasitism usually become attached while immature, whereas temporary attachment should not be expected before the male has reached sexual maturity.

An examination of the ovaries of all known material of *L. gracilispinis* (19 metamorphosed females, 10.5–103 mm) turned up 1 additional female (ROM 27284, 54 mm) approaching sexual maturity, with ovaries 8.5 mm long (15.7% SL), containing numerous eggs approximately 0.2 mm in diameter (Pietsch, 1976). A similar examination of the known material of *B. idiomorpha* (30 metamorphosed females, 11–101 mm) revealed 2 specimens with large ovaries containing ripening eggs: an 84-mm female (OSUO 1045) with ovaries approximately 15 mm long (17.8% SL) that appear to be partially spent (about one-third of the volume of each ovary consists of a tight cluster of numerous eggs, each approximately 0.3 mm in diameter; Pietsch, 1973); and a 101-mm female (SIO 92-175) with ovaries about 15 mm long (14.8% SL), containing numerous eggs, each approximately 0.2 mm in diameter.

**Thaumatichthyidae.** The family Thaumatichthyidae, containing two genera (*Lasiognathus* Regan, 1925c; and *Thaumatichthys* Smith and Radcliffe, 1912) and eight species, is represented by 65 known females, two free-living metamorphosed males, and six larvae (Bertelsen and Struhsaker, 1977; Bertelsen and Pietsch, 1996; Pietsch, 2005). There is no evidence of sexual parasitism in this family and all known specimens are sexually immature. In the largest known specimen of *Lasiognathus* (the 157-mm holotype of *L. amphirhamphus*), the ovaries are 17 mm long (10.8% SL) and contain thousands of tiny eggs, each about 0.15–0.20 mm in diameter. In the largest known females of *Thaumatichthys* (225–365 mm), the ovaries consist of a pair of relatively thin-walled sacs, each approximately 50 mm long and 15 mm wide in the 365-mm holotype of *Thaumatichthys axeli* (ZMUC P92166), and about 30 mm by 6 mm in a 294-mm specimen of *T. binghami* (USNM 21471). In both these females the slightly folded walls of the ovaries are covered with a single layer of oocytes 0.05–0.1 mm in diameter (Bertelsen and Struhsaker, 1977: 23). The testes of the metamorphosed males (31 and 36 mm; ZMUC P921946, UW 47520) are immature: smaller and of unequal length (12.8–16.7% SL) in the 36-mm specimen, about 21% SL in the 31-mm specimen (Bertelsen and Struhsaker, 1977: 26, fig. 14H). The upper and lower denticulars of the males are extraordinarily well developed, each bearing long, curved, distally hooked teeth (Bertelsen and Struhsaker, 1977: 24,

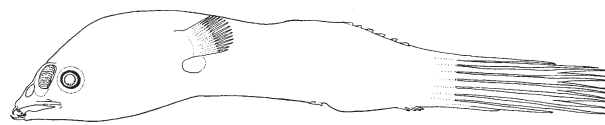


Fig. 13. Free-living male of *Thaumatichthys* sp., 31 mm, ZMUC P921946. (After Bertelsen and Struhsaker, 1977)

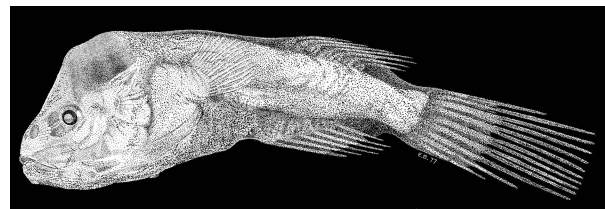


Fig. 14. Free-living male of *Centrophryne spinulosa*, 12.8 mm, SIO 70-347. (After Bertelsen, 1983)

fig. 14). The olfactory organs are relatively large as well, the length of each posterior nostril about 8–10% SL, each containing 13 olfactory lamellae (Fig. 13). The diameter of the pigmented part of the eye is 1.6–2.0 mm (5.2–5.6% SL); the diameter of the transparent outer coat of the eyeball is 2.1–2.5 mm (6.8–6.9% SL).

**Centrophrynidae.** The family Centrophrynidae, containing only *Centrophryne spinulosa* Regan and Trewavas, 1932, is now known on the basis of at least 25 metamorphosed females, three adolescent males, and two larvae. In contrast to the paired gonads of all other lophiiform fishes, female centrophrynids possess only a single oval-shaped ovary (Pietsch, 1972). Unlike the epithelial folds that line the inner walls of the ovaries of other ceratioids (Bertelsen, 1951), the lumen of the ovary of centrophrynids (three specimens examined, 136–209 mm; Pietsch, 1972) is filled with villi-like projections of the epithelium. Whole cross sections throughout the length of the ovary show small undeveloped oocytes embedded within the villi-like projections (Pietsch, 1972: 24, fig. 5). The two largest known females, a 230-mm specimen from the eastern North Atlantic (MHNLR P-811; Bertelsen and Quéro, 1981) and a 247-mm specimen from off Taiwan (ASIZP 59902), both appear to be immature, although the ovaries of the latter contain numerous developing eggs, measuring approximately 0.2–0.4 mm in diameter (Hsuan-Ching Ho, personal communication, 10 July 2004). The three known males (11.5–16 mm), two in metamorphosis and one recently metamorphosed (12.8 mm, SIO 70-347), are also immature, with testes less than 4% SL. Nevertheless, the upper and lower denticulars of these young males are well developed, each bearing three or four curved, slightly hooked teeth (Bertelsen, 1983: 314, fig. 3). The olfactory organs are relatively large, the greatest diameter of the posterior nostril of the 12.8-mm specimen measuring 7.7% SL, but the eyes are small in all three specimens compared to other ceratioid males, their diameter less than 4.5% SL (Fig. 14).

There is no evidence to support sexual parasitism in this family, but the possibility cannot be ruled out. Of particular

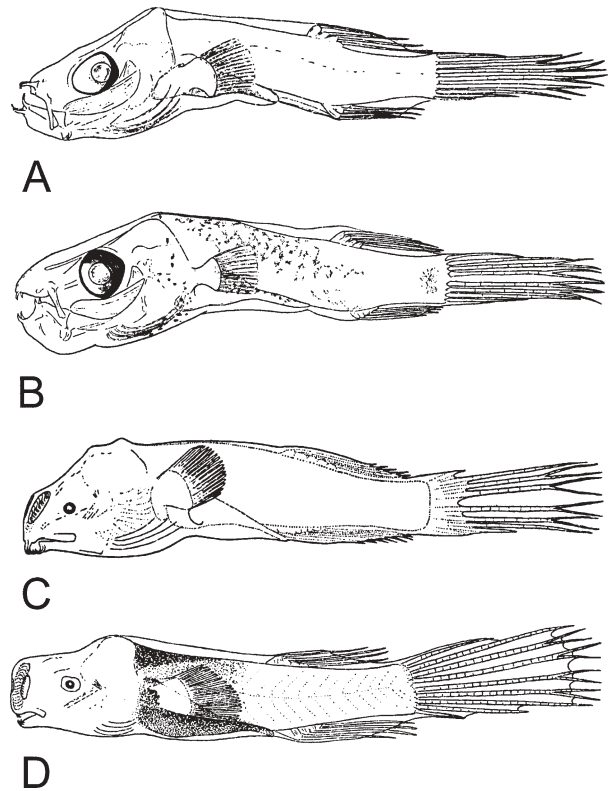


interest in this regard is the discovery of a female specimen of *Centrophryne spinulosa* (168mm SL) with an attached male of *Melanocetus johnsonii* (Pietsch and Nafpaktitis, 1971). The male is sexually mature, with large ripe testes, but there is no evidence of fusion of male–female tissue. Whether this bizarre case of possible mistaken identity occurred naturally, or whether it occurred accidentally in the net despite the small statistical probability of such an event, is unknown (Pietsch, 1976).

**Ceratiidae.** The family Ceratiidae contains two genera and four species (Pietsch, 1986). *Ceratias* Krøyer, 1845, with three species, is one of the most common and best known ceratioids, now represented by well over 300 metamorphosed females, about 75 free-living males, 37 parasitic males (attached to 35 females), and about 160 larvae (see Table 1). The genus *Cryptopsaras* Gill, 1883, with a single species, is even better known, with more than 600 metamorphosed females, at least 100 free-living males, 63 parasitic males (attached to 37 females), and about 350 larvae. As pointed out by Bertelsen (1951: 245) and reconfirmed here, all free-living *Ceratias* males are small, less than 20mm, whereas the vast majority of attached males are considerably larger, greater than 25mm SL (for the few exceptions to this general rule, see Table 1). Most weigh several times that of the largest known free-living male and a few have attained quite remarkable sizes, exceeding 140mm SL. In contrast to those of *Ceratias*, the size ranges of free-living and attached *Cryptopsaras* males overlap slightly: the largest known free-living male measures 10.5mm (14.3mm TL; Bertelsen, 1951: 144), whereas known attached males range from 9.8 (attached to a 15.5-mm female; Pietsch, 1975, 1976) to 99mm SL (Table 1).

No free-living ceratiid male with large testes has ever been found, yet large ripe testes have been described in several attached males (Regan, 1925a,b, fig. 4; Saemundsson, 1939; Bertelsen, 1943, 1951; Olsson, 1974): those of three previously unreported UW specimens (see Table 1) range from 7.3mm to about 30mm long (32.4–37.5% SL). Histological examination of the testes of two of these specimens (UW 21774, UW 21775; 20 and 34mm, respectively), showed evidence of resorption, thus indicating a recent spawning event. All known gravid females (Bertelsen, 1943, 1951; Fast, 1957; Shoemaker, 1958; Mead et al., 1964; Fitch, 1973) have a parasitic male attached. These data taken from both males and females reaffirm the idea that sexual maturity is never attained in members of this family unless stimulated by the attachment of a male.

The eyes of metamorphosed free-living males are unusually large in ceratiids, each having a prominent crescent-shaped aphakic space (Bertelsen, 1951: 127, figs. 90, 93; Munk, 1964: 5–10, figs. 1, 2; Munk, 1966: 28–30, figs. 14, 15), but they quickly degenerate upon attachment to a female. The nostrils of ceratiid males, however, are minute, in marked contrast to those of all other ceratioids (Fig. 15A,B). The general assumption that pair formation in ceratioids is mediated by a species-specific pheromone emitted by the female and tracked by the male does not appear to apply to this family.



**Fig. 15.** Free-living males of ceratiids, characterized by having small nostrils, but extremely well-developed eyes; and gigantactinids, with small eyes, but extremely large, well-developed nostrils. **A** *Ceratias* sp., 10.8mm, specimen sacrificed for histology (see Munk, 1964); **B** *Cryptopsaras couesii*, 10.2mm, specimen sacrificed for histology (see Munk, 1964); **C** *Gigantactis* male group II, 14.5 mm, ZMUC P921533; **D** *Rhynchactis* sp., 18.5 mm, ZMUC P921732. (All after Bertelsen, 1951)

The denticular jaw apparatus of metamorphosed ceratiid males is well developed, consisting of a pair of upper and two pairs of lower teeth, each elongate and slightly hooked distally, appearing quite capable of nipping onto a female, but not especially well suited for prey capture (Bertelsen, 1951: 137, 144, figs. 90, 93; Fig. 15A,B). The alimentary canal is rather poorly developed (Bertelsen, 1951: 131, 245, fig. 92). None of the specimens examined by Bertelsen (1951: 245) had food in its stomach. The few millimeters that the males increase in length during and after metamorphosis seem to result from a stretching of the body rather than any increase in body weight, and the liver decreases somewhat in size during this period. Bertelsen (1951: 245) thus concluded that free-living metamorphosed males of this family do not eat.

It was long assumed that female ceratioids, before acquiring a parasitic male, must mature to an adult stage that is of considerable size in some taxa, especially in ceratiids: “A short time . . . after metamorphosis the males become mature or ready for attachment and in these stages are more numerous than the much larger and undoubtedly much older adult females” (Bertelsen, 1951: 257; see also Regan, 1925b). But we now know that females, at least in *Cryptopsaras couesii*, may become sexually parasitized at

almost any size once past metamorphosis. Examples of small parasitized individuals include a 15.5-mm female, with a 9.8-mm male (USNM 234867); a 45-mm female, with a 10-mm male (ARC 8707665); and a 77-mm female, with a 15-mm male (BMNH 2004.6.29.4-5). In these three couples, the ovaries are as small as those found in nonparasitized females of a similar size, whereas the testes of the males are well developed, occupying more than half the volume of the coelomic cavity (1.7 mm long or 17% SL in ARC 8707665). Histological examination of the testes of the 10-mm male shows moderate resorption, thus indicating a recent spawning event. The members of the smallest attached pair appeared to be quite young, perhaps 6 months and certainly less than 12 months old.

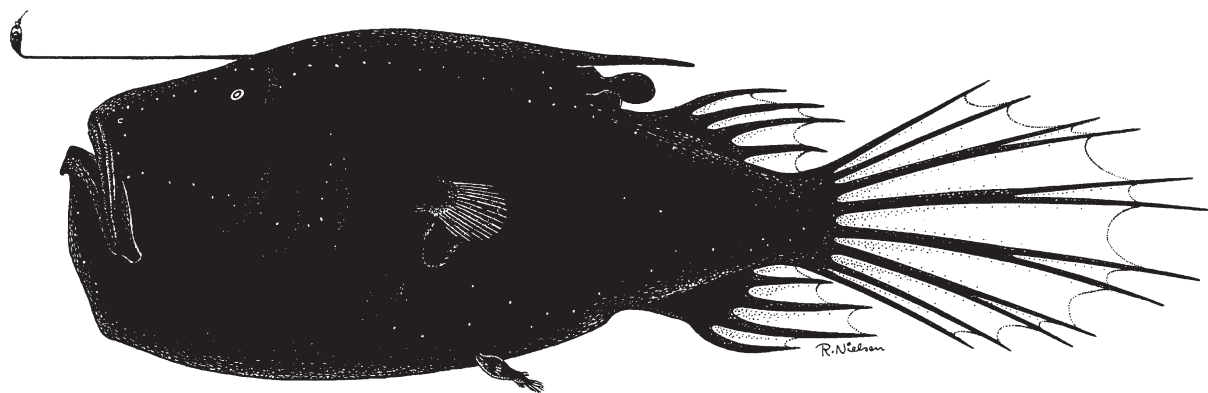
Bertelsen (1951: 250) speculated that “in one way or another, males are prevented from fixing themselves to females occupied already.” In two of the three examples of females with more than one attached male known at that time (Table 1), “the size, degree of development and stage of degeneration, are so much the same that we may believe the attachment to have taken place at the same time.” Shoemaker (1958), however, described a 176-mm *Cryptopsaras couesii* (USNM 177939) with three parasitic males that differed greatly in size; the two smaller males, 16 and 21 mm, no doubt had become attached more recently than the largest, 37-mm male. Since that time, numerous cases of multiple attachment of males at widely varying stages of development have been found in *Cryptopsaras* (as well as in some linophryniids; see Table 1). The current record is now held by a 316-mm female with eight males ranging in size from 35 to 56 mm (Saruwatari et al., 2001).

The parasitic males of *Ceratiias* are invariably attached to the belly of the female somewhat anterior to the anus; those of *Cryptopsaras* are usually found on the belly, most often offset somewhat to the right or left, but may also be placed almost anywhere on the body. Although it is difficult to say in all cases, males more often than not attach themselves upside down with respect to the surface of the female, and they are almost invariably directed anteriorly as if they approached their mate from behind (see Fig. 16).

The details of attachment of all known parasitic males of ceratiids is similar to those first described in *Ceratiias* by

Regan (1925b: 390): “In front of the mouth the snout and chin are produced forwards into outgrowths, which unite in front of the end of the lower jaw, although a groove on each side indicates the limits between them. . . . Anteriorly these outgrowths end in a swollen ring of tissue covered with naked skin, which is thicker above and below than at the sides, indicating that it is a continuation of the outgrowths of the male fish; this ring surrounds and is united to a thick stalk that projects from the female” (Figs. 3, 4, 8D). As the male grows and the extent of fusion increases, a large expansion of tissue eventually displaces the male away from the point of attachment so that a considerable distance is established between the surface of the female and the tips of the jaws of the male. In some couplings of *Ceratiias*, a nipple-like outgrowth of female tissue partially fills the mouth cavity of the male (Bertelsen, 1951: 138), but this outgrowth is never as well developed as that of the linophrynid genus *Haplophryne* (see below). In *Cryptopsaras*, more often than not, tissue fusion extends along the side of the male that comes to lie against the surface of the female, completely closing the mouth opening on that side, but always leaving the opposite side open to the gills and opercular openings. Fast (1957: 240), in his description of two males attached to a 213-mm female of *Cryptopsaras couesii* (SU 49556), found it impossible to force air through the openings of the mouth and out past the opercle, “indicating that the mass of female tissue which is taken into the mouth for attachment not only blocks off the alimentary canal but also the path of the respiratory currents.” However, upon reexamination of Fast’s (1957) specimens, a narrow probe was easily passed from the mouth and out through the gill opening. In contrast to the point of attachment of *Ceratiias* males, conspicuous flattened, circular scars (“expanded discs,” as described and figured by Shoemaker, 1958: 143, fig. 1) surround the point of attachment of those of *Cryptopsaras* (Fig. 8D).

**Gigantactinidae.** The family Gigantactinidae, containing two genera (*Gigantactis* Brauer, 1902; and *Rhynchactis* Regan, 1925c) and 21 species, is represented by at least 200 females, 50 free-living males, and 333 larvae (Bertelsen et al., 1981; Bertelsen and Pietsch, 1998). Gigantactinids are among the largest known ceratioids. Some of the 30 or so

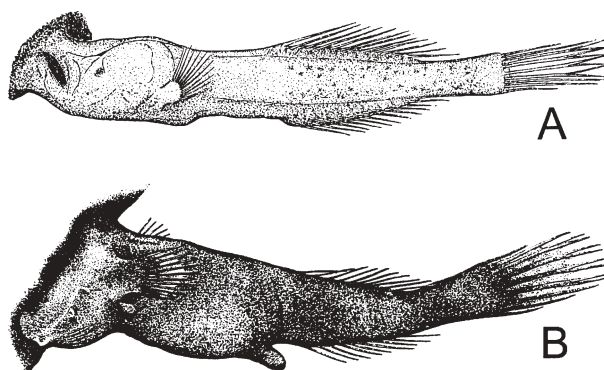


**Fig. 16.** *Cryptopsaras couesii*, 290-mm female, with 12-mm parasitic male, MCZ 29855. (Drawing by Robert Nielsen; after Bertelsen and Pietsch, 1983)

females of *Gigantactis* greater than 200 mm SL have relatively large ovaries, but none appear to be fully mature; eggs greater than about 0.5 mm in diameter have not been found. The ovaries of a 136-mm female of *Rhynchactis macrothrix* (ASIZP 61797) are about 40 mm long (30% SL) and 29 mm wide (21% SL wide), and contain about 150 000 eggs, each 0.3–0.5 mm in diameter (Hsuan-Ching Ho, personal communication, 3 May 2004). A number of *Gigantactis* males with well-developed testes, “so large that they seem to be near maturity,” have been described (Bertelsen, 1951: 153, fig. 103).

None of the females in collections around the world are parasitized by males; thus, it is assumed that males remain free-living. The largest of the known *Gigantactis* males in metamorphosis is 14.5 mm, whereas metamorphosed individuals are between 10.5 and 22 mm. This relatively large post-metamorphic increase in size indicates that these males continue to grow after metamorphosis, yet there is no evidence that post-metamorphic males are able to feed on their own; the stomachs of all metamorphosed males examined were empty (Bertelsen et al., 1981). Compared to most other ceratioids, gigantactinid males have extremely small eyes (Fig. 15C,D); diameters in most specimens are not more than 5% SL, but their nostrils are well developed, and it is thus assumed that they rely almost exclusively on olfaction to locate potential mates. The denticular jaw apparatus is well developed, consisting of long hooked teeth, two to four upper and three to five lower (Bertelsen et al., 1981: 11, figs. 14, 15, 26, 61).

**Neoceratiidae.** The family Neoceratiidae, containing only *Neoceratias spinifer* Pappenheim, 1914, is now represented by 18 metamorphosed females, seven males, and 11 larvae. All the known males are parasitically attached to females (Table 1). At least 1 of the parasitized females appears to be sexually mature or very close to it: an 86-mm female (IOAN) with ovaries 14% SL, containing numerous eggs approximately 0.6 mm in diameter (Pietsch, 1976: 789). Others are in various stages of development: a 77-mm female (AMS I.20908-002) with ovaries 14% SL, containing numerous small eggs, the largest of which measure 0.15 mm in diameter; a 42-mm specimen (LACM 34271-1) with ovaries only 4% SL, but containing numerous eggs, the largest of which are 0.2 mm in diameter; and, finally, the largest known specimen, a 108-mm female (SIO 70-336) with eggs 0.25–0.30 mm in diameter. The 15.5-mm male attached to a 52-mm female (ZMUC P921726) has testes that “are in the process of development but not remarkably large” (Bertelsen, 1951: 161). Jespersen (1984), however, found the testes of a 12.5-mm attached male (ISH 5546/79) to be exceptionally large, filling most of the abdominal cavity and containing all spermatogenic stages, spermatozoa being present in the lumina of the testes as well as in the sperm ducts. The testes of the 17.5-mm male attached to a 67.5-mm female (SIO 68-478) are 1.8 mm long (10.3% SL); those of the 18-mm male attached to the largest known specimen of the genus (108 mm, SIO 70-336) are 3.7 mm long (20.6% SL). Histological examination of the testes of the latter specimen revealed the presence of sperm, but also early resorption, indicating a recent spawning event.



**Fig. 17.** Parasitic males of *Neoceratias spinifer*. **A** 15.5 mm, attached to a 52-mm female, ZMUC P921726 (after Bertelsen, 1951); **B** 12.5 mm, attached to a 74-mm female, ISH 5546/79 (after Munk, 2000)

The peculiar denticular jaw apparatus of *Neoceratias* males appears to be poorly adapted for use in prey capture and, for that matter, seemingly unsuited for grasping a female as well (the upper element apparently absent, the lower trifurcated, each elongate arm flattened and bifurcated distally, the lateral arms curved anteriorly; see Bertelsen 1951: 157, fig. 105b; Pietsch 1976: 790, fig. 8). The eyes and olfactory structures are in an advanced state of degeneration in all the known males. In every case, the males are upside down and facing forward (with respect to the female), attached on the side and toward the posterior end of their mate, either on the caudal peduncle or between the bases of the dorsal and anal fins. One of the attached males (SIO 70-336) is located slightly anterior to the base of the anal fin, just above the anus.

In nearly all previously described examples of parasitically attached males, lateral openings to the pharynx leading to the gills and opercular openings have been found behind the area of attachment. Because the heart and gills of attached males are well developed and show no signs of degeneration even in individuals that have obviously been attached to their hosts for a considerable amount of time (Munk, 2000: 321), it has been suggested that the male does not depend on the blood of the female for oxygen, but only for nutrition (Regan, 1925b: 396; Regan, 1926: 14; Bertelsen, 1951: 245). Although one of the seven known attached males of *Neoceratias spinifer* (ZMUC P921726, Fig. 17A) has retained a large opening to the pharynx on each side (through which the teeth of the jaws can be clearly observed), the flattened dorsal surface of the head of the remaining six is broadly affixed to the side of the female (appearing as if embedded in or absorbed by the female), leaving no lateral opening into the mouth cavity (Figs. 8E, 17B). The gills of these six males, however, are as well developed as those of the seventh (and those of free-living males of other ceratioid families), perhaps indicating that sufficient oxygen is not available via the blood of the female and that this gas is extracted from water that is pumped in and out through the opercular openings (Pietsch, 1976: 790; Munk, 2000: 317; the gills of parasitic males may also remain well developed to accommodate for the elimination of CO<sub>2</sub>



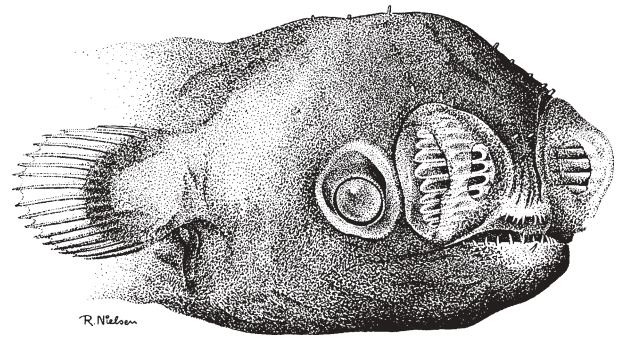
and nitrogenous waste products, the maintenance of acid-base and mineral balance, and passive diffusion of water). It might be assumed also that these latter six males represent older examples of parasitism in which the process of fusion is more complete and that over time the seventh specimen would have eventually reached a similar morphology, including complete closure of the mouth. This complete blockage of the pharynx is in sharp contrast to the situation in all other ceratioid taxa, except for the linophryinids *Haplophryne mollis* and *Photocorynus spiniceps* in which a similar occlusion appears to be present in some but not all known specimens (see below). Fast's (1957) claim that the mouth is fully occluded in an attached male of *Cryptopsaras couesii* (SU 49556) is false.

**Linophrynidae.** The Linophrynidae includes five genera and 27 species (Bertelsen, 1951, 1980a,b, 1982; Balushkin and Trunov, 1988; Gon, 1992). Four of the genera, *Acentrophryne* Regan, 1926; *Borophryne* Regan, 1925c; *Haplophryne* Regan, 1912; and *Photocorynus* Regan, 1925b, are monotypic; the fifth genus, *Linophryne* Collett, 1886, currently contains 23 species. *Borophryne*, *Haplophryne*, *Linophryne*, and *Photocorynus* are all relatively well represented in collections by metamorphosed females and free-living males, and each genus is known to have parasitic males. *Acentrophryne*, however, is known only from four metamorphosed female specimens, all of which have small undeveloped ovaries.

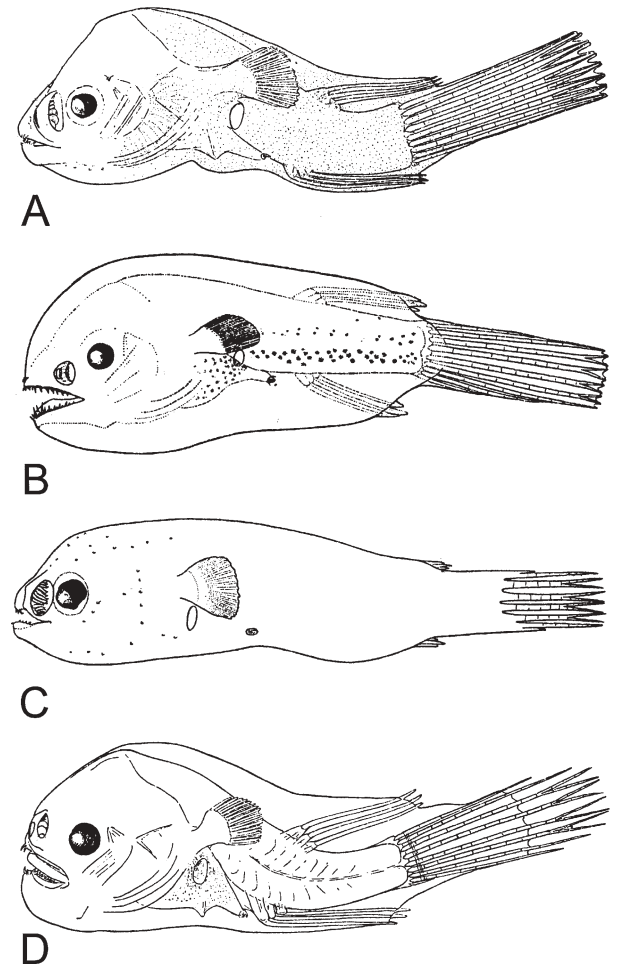
Bertelsen (1951: 247) found that the testes of all free-living linophrynid males are "less developed" than in any parasitically attached male. Males with large testes containing "numerous spermatozoa" have been found only in attached males (Regan and Trewavas, 1932: 17, fig. 6; Bertelsen, 1976: 10, 13, 15). The only known females with well-developed ovaries, many of which contain eggs that "seem almost ripe," carry an attached male (Bertelsen, 1951: 26, 1976: 10, 13, 1980a: 66; Mead et al., 1964). One of these females, a 77-mm *Linophryne arborifera*, with a 15-mm parasitic male, was found to have numerous eggs embedded in a gelatinous mass (the so-called "egg raft" or "veil," a reproductive device characteristic of all lophiiform fishes; see Pietsch and Grobecker, 1987: 351) protruding from the genital opening; the eggs, 0.6–0.8 mm in diameter, are among the largest known for any ceratioid (Bertelsen, 1980a: 66, fig. 18).

An examination of stomachs of the majority of free-living males in the Dana collections led Bertelsen (1951: 244) to consider it "extremely probable" that linophrynid males are unable to feed during their free-living stage after metamorphosis. The "short and stout" denticulars of the upper and lower jaws of these males do not "appear suitable for prey capture" (Bertelsen, 1951: 161, 205, figs. 108, 116, 117, 125). The eyes of linophrynid males are very well developed and unique among ceratioids in being tubular: Bertelsen (1951: 161, figs. 110, 112, 117, 125) described them as "telescopic, directed somewhat forward" (see also Munk, 1964: 10, fig. 1C, 2C; 1966: 31, figs. 17, 18). The nostrils of linophrynid males are also large and well developed (Figs. 18, 19).

*Borophryne*, containing only *Borophryne apogon*, is represented in collections around the world by about 30 metamorphosed females, 62 metamorphosed males (13 of which



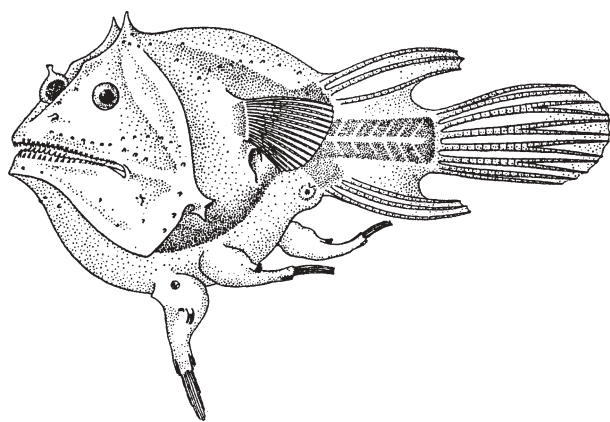
**Fig. 18.** Free-living male of *Linophryne arborifera*-group, 18.5 mm, BMNH 2004.7.5.1, showing extremely well-developed eyes and nostrils (Drawing by R. Nielsen; after Bertelsen, 1980a)



**Fig. 19.** Free-living males of linophrynids. **A** *Borophryne apogon*, 15 mm, ZMUC P921771; **B** *Haplophryne mollis*, 13 mm, ZMUC P921901; **C** *Linophryne*, 17 mm, ZMUC P921799; **D** *Photocorynus spiniceps*, 8.6 mm, ZMUC P921727. (All after Bertelsen, 1951)

are parasitically attached to females), and six larvae. Eleven of the females carry a single parasitic male, all attached in nearly the same place on the ventral midline just anterior to the anus, all upside down and directed forward with respect



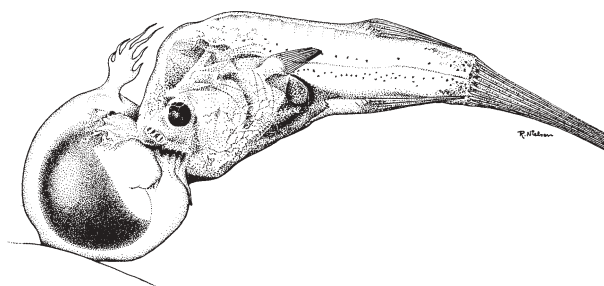


**Fig. 20.** *Haplophryne mollis*, 50-mm female, with three parasitic males, 11–12 mm, ZMUC P921777. (After Regan and Trewavas, 1932)

to the female (Table 1). A 12th female, the largest known specimen of the genus (101 mm, LACM 30053-10), has 2 attached males, both facing forward, a larger (22 mm), more heavily pigmented male situated upside down on the belly close to the anus, and a smaller (16 mm), much less pigmented male, placed right-side up, more posteriorly and slightly to the right side, at the base of the anal fin (see Pietsch, 1976: 788, fig. 7). Both these males have large testes: those of the smaller specimen, which appears to have attached itself to the female much more recently than the other, are about 2.8 mm long (17.5% SL); those of the larger male are 4.7 mm long (21.4% SL). Histological examination of the testes of the latter specimen showed evidence of late resorption, indicating a recent spawning event.

The size range of free-living *Borophryne* males is 11–17.5 mm (Fig. 19A); that of the attached males is 10.5–22 mm. Two of the parasitic males of *Borophryne*, both described by Regan and Trewavas (1932: 18, figs. 7, 8), are attached only by the tip of their lower jaw, leaving the upper jaw and its denticles more or less free (Fig. 9B), but the remaining examples are attached by both upper and lower jaws, in all cases leaving prominent openings on each side that lead into their mouths and opercular cavities. A papilla of tissue projecting from the female into the mouth of the male, as described below in *Haplophryne*, is absent.

*Haplophryne*, containing only *Haplophryne mollis*, is known from about 70 metamorphosed females, 16 metamorphosed free-living males, 42 parasitic males, and 22 larvae. Twenty-four of the females are parasitized: 11 of them carry only a single male, but 11 have 2 males, 1 has 3 (Fig. 20), and another has 6 (see Table 1). In contrast to *Borophryne* and *Linophryne* in which males are nearly always found upside down, facing forward, and attached to the belly close to the anus, those of *Haplophryne* may be found facing in any and all directions, almost anywhere on the head and trunk, and even, in one case, on the esca of the female (Munk and Bertelsen, 1983: 50, figs. 1, 3; Bertelsen and Pietsch, 1983: 96, figs. 17C, 18; see Fig. 21). In contrast also to the parasitic males of all other ceratioids (except for a few specimens of *Ceratias*; see above), a prominent nipple-

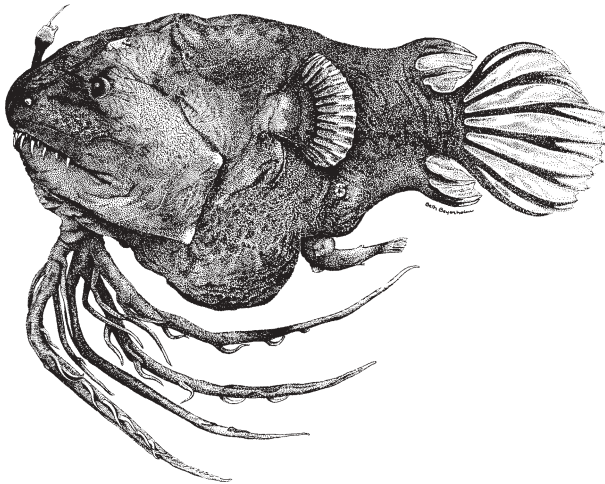


**Fig. 21.** Parasitic male of *Haplophryne mollis*, 12 mm, fused to the distal surface of the esca of a 62-mm female, AMS I.21365-8. (Drawing by Robert Nielsen; after Munk and Bertelsen, 1983)

like papilla of tissue projects from the female, more or less filling the mouth of the male (see Regan and Trewavas, 1932: 15, figs. 4, 5; Fig. 6). Munk and Bertelsen (1983: 57, 71, figs. 4, 5, 12) speculated that this papilla, if developed before actual fusion of male and female tissues, “may facilitate the earliest stages of attachment by procuring a firmer hold for the male teeth.” At the same time, however, the papilla, in filling the mouth cavity of the male, would seem to “represent a hindrance for the establishment of effective respiratory currents across the male gills.” The majority of the attached males, however, have retained an opening to the pharynx on each side, although one has lost the opening on one side, and three are so deeply embedded in female tissue that the mouth has become completely closed (ZMUC P92138; NMNZ P.26070, Andrew L. Stewart, personal communication, 8 June 2004).

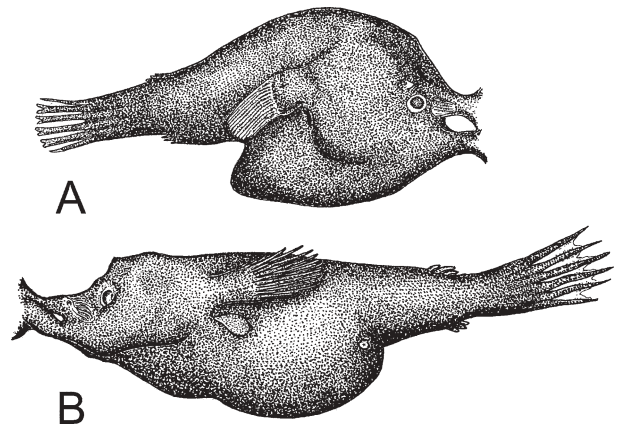
*Linophryne* is now represented in collections by a total of some 170 metamorphosed females, of which 29 carry a single parasitic male. In addition, there are about 110 known free-living males and about 80 larvae. Bertelsen (1982: 99–100) summarized the known facts surrounding sexual parasitism in this genus; his discussion follows, with only a few minor additions and updates: The 29 parasitized *Linophryne* females now known represent 12 of the 23 recognized species (Table 1). Each of these has a single male, in contrast to the linophrynid genera *Haplophryne* and *Borophryne* (and the ceratiid genera *Ceratias* and *Cryptopsaras*), in which females with two or more males are known. In all known cases, the male is directed forward with respect to the female and attached in nearly the same position on the ventral midline of the female, somewhat in front of and below the sinistral anus; with only one or two exceptions, all are attached upside down with respect to the female (Fig. 22). This is again in contrast to the linophrynid genera *Haplophryne* and *Photocorynus* (and the ceratiid genus *Cryptopsaras*) in which males may attach in any direction and almost anywhere on the head and body of the female (Munk and Bertelsen, 1983: 50, figs. 1, 3). In all known examples, the males are attached by both upper and lower jaws, leaving prominent openings on each side that lead into their mouths and opercular cavities; there is no papilla of tissue projecting from the female into the mouth of the male (Figs. 9D, 23).

Approximately half of all the known females of the genus greater than 150 mm (7 of 13) are parasitized, about one-third of the specimens ranging from 50 to 140 mm (8 of 25) are parasitized, and only a single female (42 mm) among the about 75 specimens less than 50 mm carries a parasitic male. Parasitic males considerably larger (21.5–30 mm) than any of the nearly 200 known metamorphosed free-living males of *Linophryne* (10.5–19.5 mm; see Fig. 19C) have been observed in five species (*L. lucifer*, *L. coronata*, *L. algibarbata*, *L. bicornis*, and *L. macrodon*; see Table 1), confirming that these males are true parasites most probably receiving nourishment from the blood of the females (Bertelsen 1976: 16, 1978: 31).

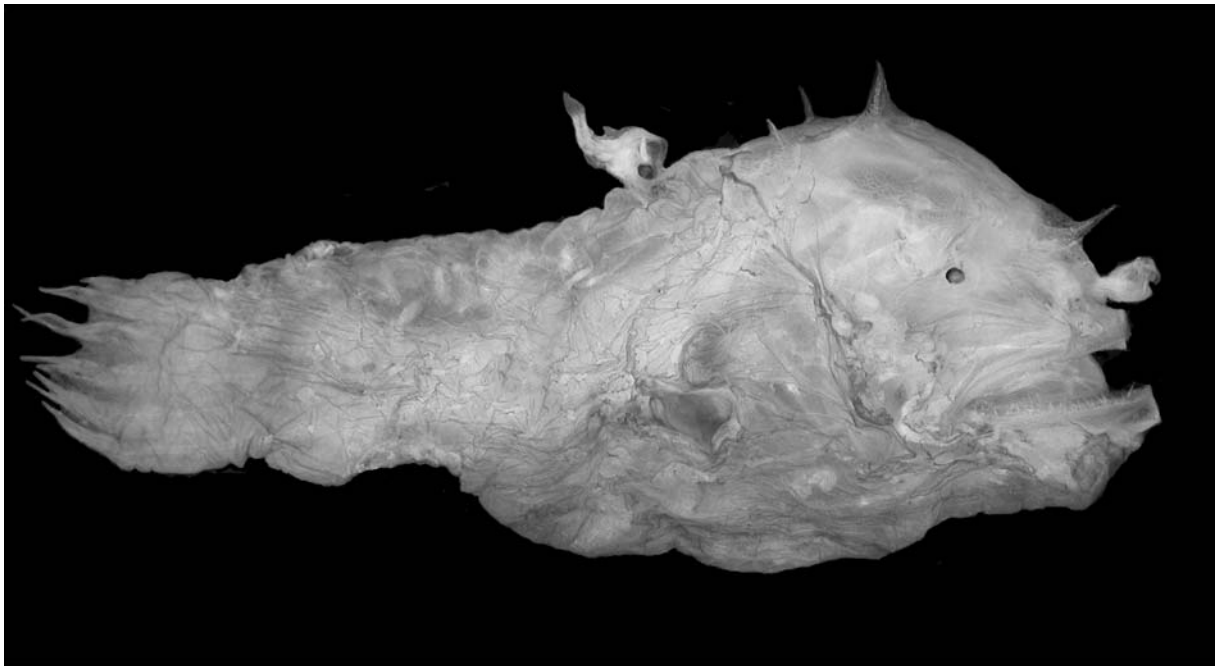


**Fig. 22.** *Linophryne brevibarbata*, 100-mm female, with an 18.5-mm parasitic male, BMNH 1995.1.18.4. (Drawing by Elisabeth Beyerholm; after Bertelsen, 1980a)

*Photocorynus*, containing only *Photocorynus spiniceps*, is now known from about 25 metamorphosed females, two free-living metamorphosed males (Fig. 19D), and four parasitic males. One of the parasitic males, a 7.4-mm specimen attached on the face just above the right eye of the 46-mm holotype of *Photocorynus spiniceps* (ZMUC P92135, Fig. 9E), was described and figured by Regan (1925b; see also Bertelsen, 1951: 166, fig. 110). The remaining three couples are reported here for the first time: ISH 1913/71, a 50.5-mm female, with a 7-mm male attached to the belly; SIO 70-326, a 46-mm female, with a 6.2-mm male attached just behind the head above the pectoral fin, slightly to the right of the dorsal mid-line (Fig. 24); and SIO 70-346, a 49-mm female,



**Fig. 23.** Parasitic males of *Linophryne*, with body cavities greatly expanded by enlarged testes. **A** *L. lucifer*, 24 mm, attached to a 230-mm female, MRIR; **B** *L. algibarbata*, 29 mm, attached to a 182-mm female, IMB. (Both after Bertelsen, 1976)



**Fig. 24.** *Photocorynus spiniceps*, 46-mm female, with a 6.2-mm parasitic male, SIO 70-326

with a 6.5-mm male in almost the same position, but slightly to the left of the dorsal mid-line. The ovaries of the ISH specimen are large and contain ripening eggs 0.4–0.5 mm in diameter, while the three remaining parasitized females appear to be immature with egg diameters of less than 0.1 mm. The belly of the 7.4-mm male attached to the holotype “is greatly inflated by the testes” (Bertelsen, 1951: 166, fig. 110C). The three newly reported parasitic males are also mature or at least close to maturity, their testes distinctly enlarged. Those of the two SIO specimens (6.2–6.5 mm) are especially well developed, their greatest length about 1.4 and 1.3 mm (22.6 and 20.0% SL, respectively), each containing large amounts of developing spermatozoa, but without evidence of flagellated sperm. Together with the 7.5-mm parasitic male of *Leptacanthichthys gracilispinis* described above, the 6.2- to 7.4-mm parasitic males of *P. spiniceps* are the smallest known within the suborder and, if regarded as adults, which histological evidence seems to indicate in the case of *Photocorynus*, they are among the world’s smallest known sexually mature vertebrates as defined in terms of length, volume, and weight (see Winterbottom and Emery, 1981; see also Roberts, 1986; Weitzman and Vari, 1988; Kottelat and Vidthayanon, 1993; Watson and Walker, 2004).

## Discussion

It has generally been assumed that male ceratioids locate conspecific females by olfactory or visual cues, or more likely by a combination of both these senses. First stated explicitly by Bertelsen (1951: 249), these ideas are supported by the fact that the eyes and olfactory structures of males are generally very well developed in free-living stages but degenerate rapidly after parasitic attachment (Bertelsen, 1951: 246; Pietsch, 1974: 98; Munk, 2000: 323): “the considerable and often enormous development of either eyes or olfactory organs or both must undoubtedly be regarded as an adaptation to the difficult task of the male to find a female. The large olfactory organs of the males indicate that the females give off specific odors. It may be assumed that the slow females leave behind them a scent, which will spread very slowly in the still water of the depths and may be perceived and followed by the searching males. Even if the eyes of the male are well developed, they can hardly observe and recognize a specific mate at any great distance, but the esca with its light organ and [species-] specific attachments may presumably function as a distinguishing mark which the males can recognize when they come sufficiently near” (Bertelsen, 1951: 249). This dual mechanism for mate location and species-specific selection probably functions in most ceratioids, in which both eyes and olfactory structures of the free-living males are well developed. But whether vision plays a significant role remains uncertain in *Himantolophus*, in which the eyes of metamorphosed males are relatively small and actually decrease slightly in diameter with increasing standard length. Furthermore, it is highly unlikely that vision and olfaction together mediate coupling in the ceratiid

genera *Cerantias* and *Cryptopsaras*, in which the nostrils are surprisingly small and undeveloped (Fig. 15A,B); and in *Centrophryne*, and especially the gigantactinid genera *Gigantactis* and *Rhynchactis*, in which the eyes are very much reduced (Figs. 14, 15C,D). However, in apparent compensation for a reduced olfactory sense, the eyes of adult free-living ceratiid males are especially large and peculiarly specialized, having an unusually wide binocular field of vision made possible by large aphakic spaces, a curved rostral part of the retina, and prominent sighting grooves (Munk, 1964: 5–10, figs. 1, 2). The unique accessory bioluminescent structures (dorsal caruncles; see Bertelsen, 1951: 16) of ceratiid females probably also play a role in what must be primarily a visually mediated mechanism of pair bonding in this family. Adult free-living gigantactinid males, on the other hand, have minute eyes, yet their olfactory structures are exceptionally large, even among ceratioids, indicating that the detection of a specific-specific pheromone emitted by the female is the dominant mode of solving the problem of coupling in this family. The eyes of centrophrynid males are also small, but there is nothing about these males that would seem to compensate for this apparent deficiency. Finally, the mechanism by which males and females of *Neocerantias* find each other remains a mystery. Although free-living males are unknown, the eyes and nostrils of all known parasitic males of this genus are especially small and degenerate, and besides these apparent deficiencies, the females lack an illicium and esca and any other known bioluminescent structure (see Bertelsen, 1951: 158, fig. 106).

All evidence indicates that the sexual parasitic mode of reproduction is obligatory in some ceratioids. Examination of available specimens of five genera (*Cerantias*, *Cryptopsaras*, *Borophryne*, *Haplophryne*, and *Linophryne*) in two families (Ceratiidae and Linophrynidae) has shown that free-living males and non-parasitized females never have well-developed gonads. Males thus apparently never mature unless they are in parasitic association with a female and, failing to locate a conspecific female within the first few months of their lives, they die. Likewise, females never become gravid until stimulated by the permanent parasitic attachment of a male. That sexual maturity is determined not by size or age in these fishes, but by parasitic sexual association, may well be unique among animals. The jaw apparatus of free-living males of these taxa seems to be unsuited to serve in prey capture and the alimentary canal is undeveloped, indicating that the males do not feed after metamorphosis and thus are fully dependent on a parasitic association with a female for long-term survival. These two lines of evidence suggest that spawning and fertilization in members of these families occur only during a permanent parasitic association of male and female. The question then arises: Why do we have so few parasitized females of these obligatory forms? Members of the genus *Cerantias* (all three species combined) are among the most commonly collected ceratioids, now known from well over 300 metamorphosed females, but only 35 or 11.7% of these specimens carry a parasitic male (see Table 1). *Cryptopsaras couesii* is even better represented in collections, with more than 600 meta-



morphosed females, but only 37 or 6.2% are parasitized. Assuming that these numbers reflect the true structure of populations at meso- and bathypelagic depths, they indicate a remarkably low percentage of individuals participating in reproduction at any one time. Furthermore, considering that females, at least in the case of *Cryptopsaras couesii*, are receptive to males at an extremely young age, beginning at a standard length of 15 mm and extending to the largest known individuals, just under 400 mm (see Pietsch, 1975; Table 1), it is reasonable to expect a higher percentage of parasitized females. It seems highly unlikely that more than 90% of the females are purely vegetative, contributing nothing to successive generations. Under these circumstances, successful recruitment on an annual basis is difficult to understand.

The ratio of parasitized to non-parasitized females of *Photocorynus spiniceps*, as represented in preserved collections, is only slightly more equitable: of the approximately 25 known metamorphosed females, 16% carry an attached male. Counts for *Haplophryne mollis* and *Borophryne apogon* are even better, with about 34% and 40% of known females parasitized, respectively. However, even in the best situation, these numbers imply that considerably more than half of all metamorphosed females are living out their lives as solitary non-reproducing individuals.

Although sufficient data are still unavailable to say with certainty, *Neoceratias* probably also reproduces by obligatory sexual parasitism. Of the 18 known metamorphosed females of this genus, 7 carry a parasitic male. At least 1 of these parasitized females is sexually mature or very close to it, and several others are in various stages of development; the 11 remaining non-parasitized females all have small ovaries without visible eggs. Although free-living males are unknown, the testes of at least one of the attached males have been shown to be exceptionally large, containing all spermatogenetic stages, with spermatozoa present in the lumina of the testes as well as in the sperm ducts. The denticular apparatus of males of *Neoceratias* is highly modified and appears essentially useless in prey capture, indicating that, similar to ceratiid and linophrynid males, those of *Neoceratias* cannot feed and therefore depend solely on a parasitic association with a female for post-metamorphic survival.

It seems evident also that males and females of some ceratioids never become associated parasitically. The Melanocetidae, Himantolophidae, Diceratiidae, Gigantactinidae, and most oneirodid genera (see Pietsch, 1976: table 1), although now well represented in collections, have yielded no evidence of male parasitism. Except in the Melanocetidae, some females of these groups have been found to contain large ovaries, with eggs visible to the naked eye; and in most all these taxa (the Melanocetidae included, but not the Diceratiidae), free-living males with large testes have been reported. Either sex is thus able to attain sexual maturity without the presence of the other. Although food items have been found in the stomachs of melanocetid males only, these and males of the Himantolophidae, Gigantactinidae, and the oneirodid genus *Oneirodes* undergo a post-metamorphic increase in length of 7–12 mm,

indicating that they are able to sustain themselves independent of the female after energy stores in their liver have been exhausted. That spawning takes place during a temporary sexual attachment, not involving fusion of male and female tissues, is supported by the presence in all these males of especially well-toothed upper and lower denticular bones that are presumably also effective in capturing prey. That collections around the world are nearly devoid of examples of temporary sexual couplings is no doubt because males are able to release themselves rather easily from their mates when startled by on-coming fishing gear. The only known exceptions are two pairs of *Melanocetus*, in which the males are firmly attached, but without tissue fusion.

The possibility that sexual parasitism may be facultative in some ceratioids, as proposed by Pietsch (1976: 791), is reaffirmed in this review. The known material of the Caulophrynidae and the oneirodid genera *Leptacanthichthys* and *Bertella* each includes at least two gravid females, one that is parasitized by a male and one that is not. Unless the non-parasitized females have somehow lost their males, leaving behind no trace, they are capable of reaching sexual maturity either with or without the presence of an attached male. These three taxa, therefore, cannot be reasonably placed within either of the two categories treated above—obligatory parasitism or non-parasitic temporary attachment. It is thus likely that fertilization of eggs can occur either during a temporary attachment or during a permanent parasitic association of male and female. Males of facultative forms probably attach to females whenever the two meet regardless of sexual readiness. If both partners are in a state of readiness at the time of attachment, spawning and fertilization take place, after which the male releases his hold on the female and is then presumably capable of beginning a new search for another mate. If one or both partners are not ready to spawn, the male remains attached until spawning can take place. The longer the male remains attached to the female, the greater are his chances of becoming fused and establishing a permanent parasitic association.

The remaining ceratioid families, Thaumactichthyidae and Centrophrynidae, still remain so poorly known that nothing can be concluded relative to their mode of reproduction. There is no evidence of sexual parasitism in either family. Although the known material contains large females in each case (225–365 and 230–247 mm, respectively), all appear to be immature. The known males of these taxa (only two and three, respectively) are also immature.

Despite major efforts over the past 25 years, no satisfactory phylogeny of ceratioid anglerfishes exists that might help to better understand the evolution of sexual parasitism. As proposed by Bertelsen (1984) and supported by morphological studies (Pietsch, 1984: 322, fig. 166; Pietsch and Grobecker, 1987: 271, figs. 110, 111), “we may assume an ogocephalid or chaunacid-like ancestral ceratioid which, from the benthic or littoral environment of its ancestors, has invaded the bathypelagic zone of the ocean. Probably this evolution passed through forms in which the adults were benthic, while the juveniles after metamorphosis continued

the pelagic life of the larvae during adolescence as, for instance, found in the family Chaunacidae and as retained or reestablished in the [benthic] ceratioid genus *Thaumatichthys*. This move to a new adaptive zone has led to a dimorphism which separates the tasks of the two sexes, the females attaining adaptations to the bathypelagic conditions of the lophiiform feeding strategy by passive luring, the males being adapted solely to actively search for a sexual partner" (Bertelsen, 1984: 330). In addition to this extreme sexual dimorphism, monophyly for the Ceratioidei is supported by a loss of the pelvic fins, a closely associated loss of the ambulatory function and a consequent re-positioning of the pectoral fins, and a general trend toward a reduction in density by a loss of bony parts, an overall decrease in ossification and the extent of muscle development, and the infusion of lipids throughout the body. The taxonomy and present classification of the suborder is based primarily on studies of the females (only 22 of the 35 recognized ceratioid genera are represented by males). Except for larval stages and the few basic meristic and osteological characters shared by both sexes, diagnoses and descriptions require separate treatment of females and males. The families of the suborder form well-defined, highly distinct taxa, separated primarily by osteological characters; the females of each family possess strikingly unique features that separate them from those of all other families (Bertelsen, 1984: 325).

Likewise, the separation and definition of genera are based primarily on characters present only in females. However, some of the distinguishing meristic and osteological characters are shared with the males, such as fin-ray counts, which in some families show distinct intergeneric differences. The structures unique to the males, such as denticular teeth and nostril morphology, show distinct intergeneric differences, in full agreement with separations based on characters of the females. But, in most cases, it has not been possible to separate free-living males into taxa below the generic level, and studies of males attached to females have not revealed characters that will allow specific identification (Bertelsen, 1984: 325).

The phylogenetic relationships among ceratioid families thus remain a puzzle, despite numerous attempts to resolve the problems (Regan, 1912, 1926; Regan and Trewavas, 1932; Bertelsen, 1951, 1984; Pietsch, 1972, 1976, 1979). Because the *Caulophrynidae* displays a number of primitive characters (for example, unlike all other ceratioids, *caulophrynid* larvae lack sexual dimorphism in the luring apparatus; adult females lack the bulbous bacteria-filled esca; and *caulophrynid* larvae retain pelvic fins, which are absent in larvae and adults of all other ceratioids), Bertelsen (1951: 28) placed this family "first in the suborder." At the same time, he argued that *linophrynids* show "such a highly specialized condition that they must be placed last." Because members of both these families are characterized by having parasitic males, Bertelsen's (1951) classification requires that sexual parasitism evolved at least twice within the suborder. For unstated reasons, Greenwood et al. (1966: 397) implied a much closer relationship between the *Caulophrynidae* and *Linophrynidae*. Likewise, Pietsch

(1975, Annual Meeting of the American Society of Ichthyologists and Herpetologists at Williamsburg, Virginia) reported numerous derived character states shared by these two families as well as with the *Gigantactinidae* and *Neoceratiidae*. He presented a phylogeny that argued for a monophyletic origin of sexual parasitism within a lineage derived from some oneirodid-like ancestor (Pietsch, 1976: 791; see also Pietsch, 1979: 22, figs. 25, 26). In the most recent attempt to determine the phylogenetic relationships of ceratioid taxa, Bertelsen (1984: 331) summed up the problem by stating that "most of the derived osteological characters shared by two or more families are reduction states or loss of parts . . . and similarities among such characters may in many cases represent convergent developments. At the same time, most of the diagnostic family characters which represent new structures or specialization of organs are autapomorphic." Nevertheless, Bertelsen (1984: 333, fig. 171) was able to throw new light on the subject, presenting a cladogram that, in contrast to that published by Pietsch (1979), indicates that sexual parasitism evolved at least three and perhaps four times within the suborder. Bertelsen (1984: 334) concluded that "ceratioids are still very incompletely known and future studies on additional characters and as yet unknown forms may bring answers to at least some of the many questions about their phylogenetic relationships."

Recent and on-going attempts to determine ceratioid relationships through analysis of DNA are providing good results. The first of two separate studies is a comparison of the mitochondrial 16S rRNA gene for 16 lophiiform genera, representing 11 families and all anglerfish suborders, and a region of the mitochondrial *cyt b* gene for a subset of these taxa (Shedlock et al., 2004). Results are markedly different from those of Bertelsen (1984), yet some clear similarities exist. Of special interest is the lack of support for a monophyletic origin of sexual parasitism. The data suggest instead an abrupt appearance and subsequent loss of sexual parasitism during ceratioid evolution, followed by a secondary gain in the *Oneirodidae*. The apparent plasticity of this life history strategy is more consistent with the multiple gains and losses of parasitism required by Bertelsen's (1984) hypothesis (Shedlock et al., 2004). A second study, still in its preliminary stages (Miya et al., in preparation), is corroborating these findings but, at the same time, providing more details. Based on a partitioned Bayesian analysis of whole mitochondrial genome sequences of 47 lophiiform species, including representatives of all 11 ceratioid families, the results so far also fail to support a monophyletic origin of sexual parasitism, indicating instead multiple appearances and several subsequent losses. In summary, no matter how we look at ceratioid phylogeny, whether based on comparative morphology or molecular analysis, results indicate that sexual parasitism has evolved multiple times independently within the suborder.

These findings are consistent with the many differences evident in the precise nature of attachment among the various taxa: males attached to the apex of an unpigmented conical growth from the female in *Caulophryne*; fused to the tip of a cylindrical stalk of female tissue in the oneirodid

genera *Bertella* and *Leptacanthichthys*; nearly always single males attached invariably on the belly in *Ceratias*, but multiple males found almost anywhere on the body in *Cryptopsaras*; broadly attached males, with fully occluded mouths in *Neoceratias*; multiple males common in *Haplophryne*, attached anywhere on the head and body, and always involving a papilla of female tissue that fills the mouth of the male; and, finally, single males always the rule in *Linophryne*, almost always attached upside down at nearly the same spot on the ventral mid-line of the female. Having been established independently three and possibly as many as five times within the suborder, it seems evident, yet difficult to believe, that sexual parasitism in ceratioid anglerfishes, with all its extreme complexity of morphological, physiological, and behavioral adaptations, is a considerably less drastic evolutionary event than might be supposed. When viewed in this light, it is perhaps surprising that this remarkably successful reproductive strategy has not evolved in other vertebrate taxa that have come to occupy the deep sea.

### Summary and Conclusions

1. Knowledge of ceratioid reproductive biology is historically reviewed and brought up to date.
2. Additional examples of parasitized females are listed and described, bringing the total number in collections around the world to 155.
3. Examples of temporary attachment of ceratioid males are described for the first time, one in *Melanocetus johnsonii* and another in *Melanocetus murrayi*.
4. Sexual parasitism is described for the first time in *Bertella idiomorpha*, the second known occurrence of parasitism in the family Oneirodidae and the first record of a male for the genus.
5. Extremely young sexually parasitized females of *Cryptopsaras couesii* indicate that females of this species are able to elicit a search response in a conspecific male, as well as provide cues for specific identification by the male at a very early age.
6. There is no mechanism that prevents additional males from becoming attached to a previously parasitized female, but *Linophryne* (and perhaps *Caulophryne*), in which multiple attachments have so far not been found, might be an exception to this rule. Multiple attachment is rare in *Ceratias* and *Borophryne* (only a single record of two males in each case), but common in *Cryptopsaras* and *Haplophryne*, which are known to have as many as eight and six males, respectively.
7. Males are almost invariably attached upside down and facing forward with respect to the female, and almost always on the ventral midline of the belly of the female, somewhat anterior to the anus; exceptions include those of *Cryptopsaras*, *Haplophryne*, and *Photocorynus*, which may be found almost anywhere on the head and body, and oriented in any direction.
8. Six of the seven known parasitically attached males of *Neoceratias spinifer* lack openings to the pharynx leading to the gills and opercular openings, which are present in the area of attachment of nearly all previously described examples of attached males (exceptions include several attached males of *Haplophryne mollis*). The gills of these *Neoceratias* males, however, are as well developed as those of free-living males of other ceratioid families, indicating that sufficient oxygen is probably not available via the blood of the female and that this gas is extracted by water that is pumped in and out through the opercular openings.
9. The 7.5-mm parasitic male of *Leptacanthichthys gracilispinis* and the 6.2- to 7.4-mm parasitic males of *P. spiniceps* are the smallest to be found within the suborder and, if regarded as adults, which histological evidence confirms in the case of *Photocorynus*, they are among the world's smallest known sexually mature vertebrates as defined in terms of length, volume, and weight.
10. A dual mechanism for mate location and species-specific selection probably functions in most ceratioids, in which both eyes and olfactory structures of the free-living males are well developed, but it is highly unlikely to function in the ceratiid genera *Ceratias* and *Cryptopsaras*, in which the nostrils are surprisingly small and undeveloped, and in *Centrophryne* and the gigantactinid genera *Gigantactis* and *Rhynchactis*, in which the eyes are very much reduced. The mechanism by which males of *Neoceratias* (in which the eyes and nostrils are especially small and degenerate) find females (which apparently lack bioluminescent structures) remains a mystery.
11. The parasitic mode of reproduction is apparently obligatory in *Ceratias*, *Cryptopsaras*, *Borophryne*, *Haplophryne*, and *Linophryne*, and, although sufficient data are lacking to say for certain, probably in *Neoceratias* as well.
12. Males of those taxa in which sexual parasitism is obligatory apparently never mature unless they are in parasitic association with a female, and, likewise, females never become gravid until stimulated by the permanent parasitic attachment of a male. That sexual maturity is determined not by size or age in these fishes, but by parasitic sexual association, may well be unique among animals.
13. Among those taxa in which parasitism seems to be obligatory, the number of parasitized females in collections around the world is surprisingly small compared to the total number of known specimens: about 6% in *Cryptopsaras*, 11% in *Ceratias*, 16% in *Photocorynus*, 33% in *Haplophryne*, and 40% in *Borophryne*.
14. Males of the Melanocetidae, Himantolophidae, Diceratiidae, Gigantactinidae, and several of the better known oneirodid genera (for example, *Oneirodes*, *Microlophichthys*, *Dolopichthys*, *Chaenophryne*, and *Lophodolos*, each now known from well over 50 females), probably never become parasitic. Spawning and fertilization may take place during a temporary sexual attachment that does not involve fusion of male and female tissues.



15. Sexual parasitism is probably facultative in *Caulophryne* and in the oneirodid genera *Bertella* and *Leptacanthichthys*.
16. The remaining ceratioid families, Thaumathichthyidae and Centrophrynidae, are still so poorly known that little can now be concluded concerning their mode of reproduction.
17. Phylogenetic evidence from comparative morphological and molecular analyses indicates that sexual parasitism has evolved multiple times within the Ceratioidei, but a definitive picture of the evolution of this complex and intriguing life history strategy must await the discovery of additional material of rare taxa for which reproductive modes are presently unknown.

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