









Deep-sea anglerfishes (Lophiiformes: Ceratioidei) from off northeastern Brazil, with remarks on the ceratioids reported from the Brazilian Exclusive Economic Zone

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The deep-sea anglerfishes of the suborder Ceratioidei (Lophiiformes) are represented by about 170 valid species with some of the most extraordinary morphological and reproductive adaptations among vertebrates, including extreme sexual dimorphism and male parasitism. Here we report on the diversity and distribution of rare ceratioids collected during the ABRACOS (Acoustics along the BRAzilian COaSt) expeditions off northeastern Brazil and the Fernando de Noronha Ridge (Rocas Atoll, Fernando de Noronha Archipelago, and associated seamounts). *Chaenophryne ramifera*, *Oneirodes anisacanthus*, *O. carlsbergi*, *Gigantactis watermani*, and unidentified specimens of *Caulophryne*, *Dolopichthys*, and *Rhynchactis* are recorded for the first time in the Brazilian Exclusive Economic Zone. *Ceratias uranoscopus*, *Melanocetus johnsonii*, and *Chaenophryne draco* have their distributions extended in Brazilian waters. *Caulophryne*, *O. anisacanthus*, and *G. watermani* are also recorded for the first time in the western South Atlantic. The specimen of *G. watermani* reported here represents the third known specimen of the species, and variations of its esca anatomy in relation to the holotype are described. Based on specimens examined and a review of records in the literature, 20 species of the Ceratioidei, in addition to unidentified species of *Caulophryne*, *Dolopichthys*, and *Rhynchactis*, are confirmed in the Brazilian Exclusive Economic Zone.

Keywords: Distribution, Fernando de Noronha Archipelago, Rocas Atoll, Seamounts, Taxonomy.

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Os peixes-pescadores de profundidade da subordem Ceratioidei (Lophiiformes) são representados por cerca de 170 espécies válidas que apresentam algumas das adaptações anatômicas e reprodutivas mais extraordinárias entre os vertebrados, incluindo extremo dimorfismo sexual e parasitismo masculino. No presente estudo reportamos sobre a diversidade e distribuição de espécies raras de Ceratioidei coletadas durante as expedições ABRACOS (*Acoustics along the BRAzilian COaSt*) realizadas ao largo do nordeste do Brasil e na Cadeia de Fernando de Noronha (Atol das Rocas, Arquipélago de Fernando de Noronha e montes submarinos associados). *Chaenophryne ramifera*, *Oneirodes anisacanthus*, *O. carlsbergi*, *Gigantactis watermani* e espécimes não identificados de *Caulophryne*, *Dolopichthys* e *Rhynchactis* são registrados pela primeira vez na Zona Econômica Exclusiva brasileira. *Ceratias uranoscopus*, *Melanocetus johnsonii* e *Chaenophryne draco* tiveram suas distribuições estendidas em águas brasileiras. *Caulophryne*, *O. anisacanthus* e *G. watermani* também são registrados pela primeira vez no Atlântico Sul ocidental. O espécime de *G. watermani* reportado aqui representa o terceiro espécime conhecido da espécie, e variações anatômicas de sua esca em relação à do holótipo são descritas. Com base nos espécimes examinados e na revisão de registros na literatura, 20 espécies de Ceratioidei, além de espécies não identificadas de *Caulophryne*, *Dolopichthys*, and *Rhynchactis*, são confirmadas na Zona Econômica Exclusiva brasileira.

Palavras-chave: Arquipélago de Fernando de Noronha, Atol das Rocas, Distribuição, Montes submarinos, Taxonomia.

INTRODUCTION

The Ceratioidei (Lophiiformes) includes 11 families, 35 genera and about 170 valid species of fishes commonly known as deep-sea anglerfishes (Pietsch, Orr, 2007; Pietsch, 2009; Ho, Shao, 2019; Fricke *et al.*, 2021). Adults and larvae of the group are remarkable in a number of features, including their anatomical diversity and extreme sexual dimorphism in which males are often obligatorily attached to females, with fusion of tissues and sharing of circulatory systems (Pietsch, 2009; Swann *et al.*, 2020). Members of the Ceratioidei are also externally recognized by the absence of pelvic fins, scales usually absent (but prickles, spines or plates variably present), gill openings narrowly constricted and forming a tube-like structure that opens posteriorly, denticular bones present in dwarf males, usually 12–28 pectoral-fin rays, 8–9 caudal-fin rays, and females with an illicial apparatus usually tipped by a modified esca containing a globular, bacteria-filled photophore (Pietsch, 2009). Female ceratioids are also typically short and deep, with a nearly globular body in the Caulophrynidae, Melanocetidae, Himantolophidae, Diceratiidae, and Linophrynidae, or with a more elongate and somewhat laterally compressed body in the Centrophrynidae, Ceratiidae, Gigantactinidae, Neoceratiidae, Thaumatchthyidae, and some members of the Oneroididae (Pietsch, 2009).

Despite representing one of the most ubiquitous deep-sea groups of vertebrates in the meso- and bathypelagic zones, new species of deep-sea anglerfishes continue to

be described, mostly from still poorly explored regions of the world (Ho, Shao, 2004; Stewart, Pietsch, 2010; Pietsch, Kenaley, 2011; Prokofiev, 2014a,b; Ho *et al.*, 2016; Rajeeshkumar *et al.*, 2017; Ho, Shao, 2019). With about 7,500 km of coastline in addition to some biogeographically relevant oceanic island complexes (Reis *et al.*, 2016), the Brazilian Exclusive Economic Zone (EEZ) stands out in the western South Atlantic as one of such poorly known regions in terms of its deep-sea biota. Indeed, this area includes several Ecologically or Biologically Significant Marine Areas that encompass hotspots of biodiversity and endemism (CBD, 2014).

Part of the northeastern Brazilian coast and adjacent oceanic islands and seamounts were recently explored by the RV *Antea*, resulting in the collection of more than 9,000 specimens of mesopelagic fishes (Bertrand, 2015, 2017). Studies based on these collections have contributed significantly to the understanding of the deep-sea fauna of different groups in the region (Eduardo *et al.*, 2018, 2019, 2020a,b; Mincarone *et al.*, 2019, 2020; Afonso *et al.*, *in press*). This study, part of an ongoing effort to report on the still puzzling deep-sea fauna of the western South Atlantic, focus on the diversity of deep-sea anglerfishes collected off northeastern Brazil, including oceanic islands and seamounts. Remarks on the taxonomy and distribution of previous records of the Ceratioidei in the Brazilian EEZ are also presented.

MATERIAL AND METHODS

Specimens examined in this study are part of a large collection of mesopelagic invertebrates and fishes collected during the ABRACOS expeditions (Acoustics along the BRAZilian COaSt), carried out between 30 September and 20 October 2015 (ABRACOS 1 - AB1; Bertrand, 2015), and between 9 April and 6 May 2017 (ABRACOS 2 - AB2; Bertrand, 2017). Both expeditions were conducted onboard the French RV *Antea* off Rio Grande do Norte to Pernambuco States and along the Fernando de Noronha Ridge, formed by the Fernando de Noronha Archipelago, the Rocas Atoll, and the seamounts off Rio Grande do Norte and Ceará States (Jinno, Souza, 1999). The survey comprised 82 fishing stations, between the surface and 1,113 m depth. Sampling was conducted using micronekton (body mesh 40–80 mm, cod-end mesh 10 mm, height 24 m, width 24 m) and mesopelagic (body mesh 30 mm, cod-end mesh 4 mm, height 8.4 m, width 12.6 m) nets. Trawl depth was continuously recorded using a Scanmar depth sensor fitted on the upper part of the trawl mouth. An open-mouth net was employed, but collection of specimens most likely occurred at pre-established target depths, which were defined for each trawl according to the presence of an acoustic scattered layer or patches detected with a Simrad EK60 split-beam scientific echo sounder. At the target depths, trawling activity lasted for about 30 minutes. Target depth is therefore indicated as capture depth in the species accounts presented herein. Specimens were identified based on Pietsch (2009). Only female specimens were examined and, unless stated otherwise, distributional data refers to female specimens. All specimens collected were deposited in the Fish Collection of the Instituto de Biodiversidade e Sustentabilidade, Universidade Federal do Rio de Janeiro (NPM, Macaé, Brazil). Other institutional abbreviations follow Sabaj (2020).

RESULTS

CERATIIDAE

Females of the Ceratiidae are distinguished by having an elongate, laterally compressed body; mouth almost vertical to strongly oblique; 2 or 3 club-shaped caruncles (low fleshy appendages) on the dorsal midline just anterior to the soft dorsal fin; dorsal-fin rays 4 or (rarely) 5; 4 anal-fin rays; 15–19 pectoral-fin rays; caudal fin rounded, with 8 well-developed rays (the ninth or lower-most ray reduced to a small remnant in *Ceratias*); the pterygiophore of the illicium emerging anteriorly well behind the tip of the snout and posteriorly on the back, near the soft dorsal-fin origin; males obligatory sexual parasites as adults (Pietsch, 2009).

Ceratias Krøyer, 1845

Diagnosis. *Ceratias* differs from *Cryptopsaras*, the only other genus of the Ceratiidae, by having 9 caudal-fin rays, the ninth or ventral-most ray reduced to a small remnant (*vs.* 8 caudal-fin rays), and by the absence of a spine on the anterodorsal margin of the subopercle (Bertelsen, 1951; Pietsch, 1986, 2009). Metamorphosed females of *Ceratias* are further differentiated from those of *Cryptopsaras* by having a long illicium, 19.0–28.2% SL (*vs.* illicium reduced to a small remnant, nearly fully enveloped by tissue of the esca), and by the number of club-shaped caruncles on the dorsal midline of the trunk just anterior to the origin of the soft dorsal fin (2 *vs.* 3) (Pietsch, 1986, 2009).

Ceratias uranoscopus Murray, 1877

(Figs. 1A, 2)

Diagnosis. Metamorphosed females of *Ceratias uranoscopus* differ from those of *C. holboelli* Krøyer, 1845 and *C. tentaculatus* (Norman, 1930), the other two known species of the genus, by the absence of distal esca appendages (*vs.* presence of a single distal esca appendage or a pair of distal esca appendages), and by the lack of vomerine teeth (*vs.* present or nearly always present) (Pietsch, 1986, 2009).

Geographical distribution. *Ceratias uranoscopus* is widely distributed in the Atlantic and Pacific. It is also known from the Indian Ocean based on three specimens collected off South Africa, India, and the Arabian Sea (Pietsch, 1986, 2009; Rajeeshkumar *et al.*, 2016). In the Atlantic, it is reported from off Nova Scotia in the west to approximately 40°S off Cape Town in the east (Pietsch, 2009). The species was previously reported in Brazilian waters based on a specimen (129 mm SL) collected off southeastern Saint Peter and Saint Paul Archipelago (MCZ 42845, 0°03'N 27°31'W) (Pietsch, 1986; Menezes *et al.*, 2003; Melo *et al.*, 2020). In the present study, a single specimen is reported nearby Fernando de Noronha Archipelago, at 850 m depth (Fig. 2).

Remarks. Three additional small (31–51 mm SL) specimens of *Ceratias* (NPM 4974, NPM 4978, NPM 4979) were also collected during the ABRACOS expeditions, but

identification was only possible to genus. They were collected around Rocas Atoll (610 m depth) and near the seamounts off Rio Grande do Norte State (670–700 m depth) (Fig. 2).

In addition to *Ceratias uranoscopus*, *C. holboelli* and *C. tentaculatus* were previously reported in the western South Atlantic (Sutton *et al.*, 2008; Porteiro *et al.*, 2017). *Ceratias holboelli* is widely distributed in the Atlantic and Indo-Pacific, with records in the Atlantic ranging between 68°N and 14°S. The species was recorded in Brazilian waters based on a single specimen collected off Ilhéus, Bahia State (MNRJ 30701, 14°36'36"S 38°49'21"W; Pietsch, 2009; Fig. 2). This specimen was previously identified as *C. uranoscopus* by Costa *et al.* (2007). Melo *et al.* (2020) also listed *C. uranoscopus* in Brazilian waters based on this misidentification. *Ceratias tentaculatus* is restricted to the Southern Hemisphere with two records in the western South Atlantic, one off northern Argentina (ISH 435/71, 38°20'S 54°33'W), and another off Rio Grande do Sul State, close to the Brazilian EEZ (ISH 1657/68, 35°16'S 49°26'W) (Pietsch, 1986). *Ceratias tentaculatus* has also been briefly mentioned as occurring off Uruguay (Nión *et al.*, 2016).

Cryptosaras couesii Gill, 1883 is known from the Atlantic, Indian and Pacific Oceans (Pietsch, 2009). The species was also reported in Brazilian waters based on specimens collected off Pará State (MCZ 147828, 01°24'N 45°24'W) and off Saint Peter and Saint Paul Archipelago (MCZ 45065, 00°58'S 27°34'W; MCZ 76502, 00°34'N 30°43'W) (Pietsch, 1986; Edwards, 1993; Menezes *et al.*, 2003; Sutton *et al.*, 2008; Pietsch, 2009; Porteiro *et al.*, 2017; Melo *et al.*, 2020; Fig. 2). Larvae of *C. couesii* have also been recently reported off Trindade Island (20°27'36"S 29°26'16"W; Stocco, Joyeux, 2015).

Material examined. NPM 5060, 1, 76 mm (Fig. 1A), RV *Antea*, sta. AB2/44A, 3°52'52.5"S 32°17'33.3"W to 3°52'13.4"S 32°16'28.0"W, 850 m, 28 Apr 2017, 12:44–13:17 h.

HIMANTOLOPHIDAE

Females of the Himantolophidae are distinguished by having a short, deep, globular body; lower jaw unusually blunt, extending anteriorly beyond the upper jaw; illicium thick and stout, esca unusually large and anatomically complex, the pterygiophore of the illicium fully embedded in the dermis of the head; low and rounded wart-like papilla covering the snout and chin; sphenotic spines well developed, spines absent on quadrate, articular, angular and preopercular bones; jaw teeth numerous and short, arranged in several close-set longitudinal series, vomer broad and toothless; skin of specimens larger than 30–40 mm SL, with large, widely spaced bony plates, each bearing a single median spine; 5–6 dorsal-fin rays, 4 anal-fin rays, 14–18 pectoral fin-rays, 9 caudal-fin rays; males free-living, apparently never parasitic on females (Bertelsen, Krefft, 1988; Pietsch, 2009).

Himantolophus Reinhardt, 1837

Diagnosis. *Himantolophus* is the only genus in the family. In addition to the diagnostic features of the Himantolophidae, females and males are distinguished by the absence of the parietal bone throughout life (*vs.* parietal present or lost during metamorphosis in females of the gigantactinid genus *Rhynchactis*), and by the presence of a triradiate pelvic bone (sometimes also present in the oneirodid genus *Chaenophryne*) (Pietsch, 2009).

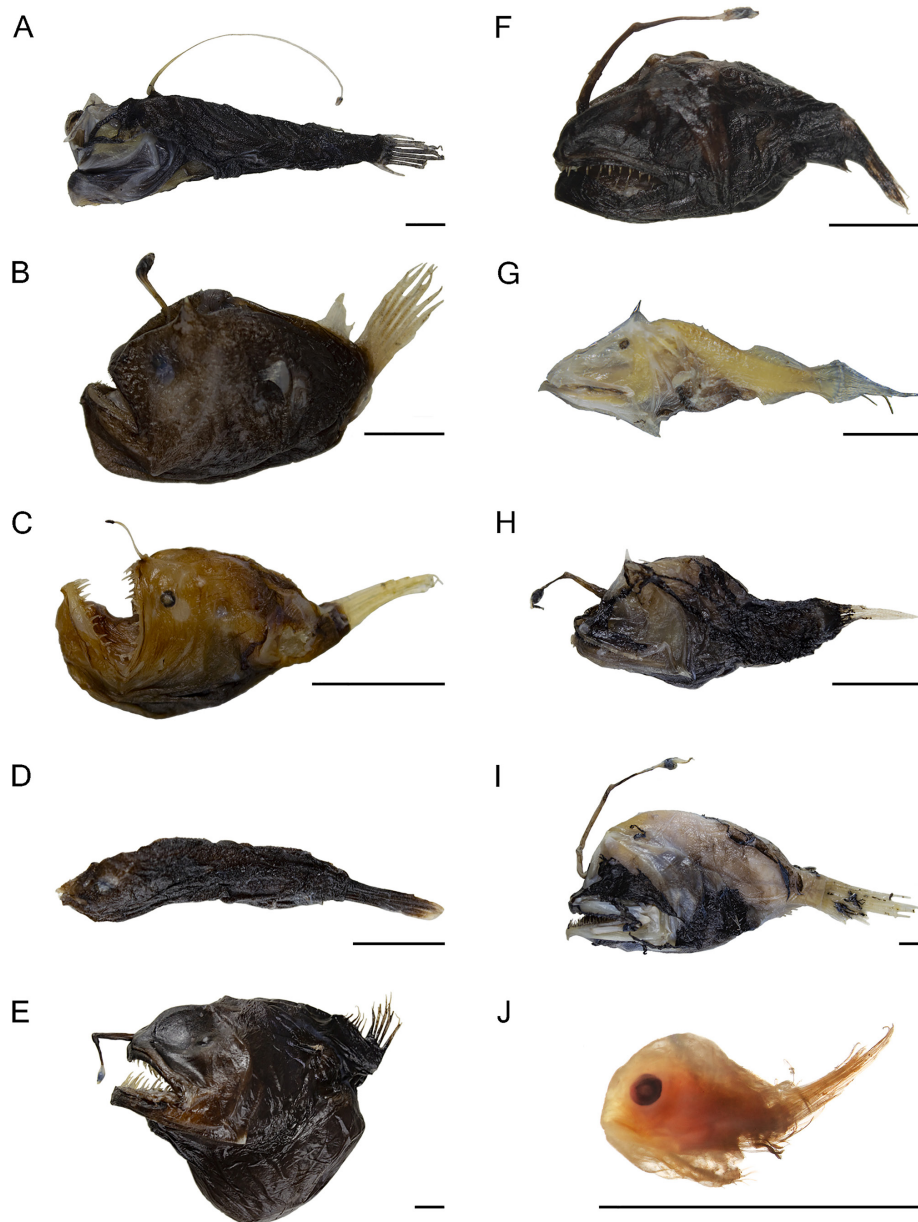


FIGURE 1 | Species of the Ceratioidei reported in this study: **A.** *Ceratias uranoscopus*, NPM 5050, 76 mm SL; **B.** *Himantolophus* sp., NPM 4959, 37 mm SL; **C.** *Melanocetus johnsonii*, NPM 4970, 19 mm SL; **D.** *Thaumatoichthys* sp., NPM 4985, 32 mm SL; **E.** *Chaenophryne draco*, NPM 4954, 90 mm SL; **F.** *Chaenophryne ramifera*, NPM 4955, 32 mm SL; **G.** *Dolopichthys* sp., NPM 4980, 35 mm SL; **H.** *Oneirodes anisacanthus*, NPM 4977, 30 mm SL; **I.** *Oneirodes carlsbergi*, NPM 4953, 98 mm SL; **J.** *Caulophryne* sp., NPM 3835, 6 mm SL. Scale bars = 10 mm.

Himantolophus sp.

(Figs. 1B, 2)

Geographical distribution. A total of 13 larvae and juvenile specimens were collected off Rio Grande do Norte State, the Fernando de Noronha Archipelago, Rocas Atoll, and the seamounts off Rio Grande do Norte State, between 35 and 1,113 m (Fig. 2).

Remarks. Due to the immature nature of the specimens collected in this study, identification was possible only to genus. It is also possible that those specimens represent more than one species. *Himantolophus* currently includes 20 species distributed among five species groups, with representatives of all groups occurring in the Atlantic Ocean (Bertelsen, Krefft, 1988; Pietsch, 2009; Stewart, Pietsch, 2010; Pietsch, Kenaley, 2011; Fricke *et al.*, 2021). Two species of *Himantolophus* were previously reported in Brazilian waters: *Himantolophus macroceras* Bertelsen & Krefft, 1988, known from five specimens reported from the central Atlantic, including one collected off Saint Peter and Saint Paul Archipelago (MCZ 58177, 0°10'N 27°30'W; Bertelsen, Krefft, 1988); and *Himantolophus groenlandicus* Reinhardt, 1837, widely distributed in the Atlantic, with one specimen reported off Saint Peter and Saint Paul Archipelago (MCZ 49841, 1°02'N 29°04'W; Bertelsen, Krefft, 1988; Fig. 2). A third species, *Himantolophus paucifilosus* Bertelsen & Krefft, 1988, might also occur off Brazil (Melo *et al.*, 2020; see Discussion).

Material examined. NPM 3840, 1, 9.5 mm, RV *Antea*, sta. AB1/5, 4°05'23.9"S 32°10'49.0"W to 4°04'33.4"S 32°11'53.1"W, 85 m, 2 Oct 2015, 21:18–22:48 h; NPM 3841, 3, 8.5–13 mm, RV *Antea*, sta. AB1/12, 3°56'19.0"S 33°30'39.2"W to 3°56'35.8"S 33°32'00.3"W, 130 m, 5 Oct 2015, 21:24–21:54 h; NPM 4959, 1, 37 mm (Fig. 1B), RV *Antea*, sta. AB2/39, 4°52'26.9"S 34°35'22.9"W to 4°50'52.8"S 34°51'04.7"W, 650–800 m, 24 Apr 2017, 21:49–22:37 h; NPM 4961, 1, 24 mm, RV *Antea*, sta. AB2/42A, 3°15'28.1"S 31°48'29.1"W to 3°15'27.8"S 31°50'40.6"W, 780 m, 27 Apr 2017, 12:23–12:26 h; NPM 4964, 1, 21 mm, RV *Antea*, sta. AB2/44A, 3°52'52.5"S 32°17'33.3"W to 3°52'13.4"S 32°16'28.0"W, 850 m, 28 Apr 2017, 12:44–13:17 h; NPM 4968, 1, 24 mm, RV *Antea*, sta. AB2/49A, 4°10'38.1"S 33°16'07.4"W to 4°10'58.0"S 33°15'03.8"W, 770–1020 m, 30 Apr 2017, 21:17–21:52 h; NPM 4973, 1, 19 mm, RV *Antea*, sta. AB2/53A, 3°48'58.7"S 33°59'17.1"W to 3°50'05.8"S 33°58'46.5"W, 610 m, 2 May 2017, 22:08–22:40 h; NPM 4982, 1, 29 mm, RV *Antea*, sta. AB2/59A, 3°38'01.6"S 36°31'46.3"W to 3°38'36.1"S 36°17'49.7"W, 700–1113 m, 5 May 2017, 21:57–22:37 h; NPM 4984, 1, 30 mm, RV *Antea*, sta. AB2/59A, 3°38'01.6"S 36°31'46.3"W to 3°38'36.1"S 36°17'49.7"W, 700–1113 m, 5 May 2017, 21:57–22:37 h; NPM 5221, 1, 18 mm, RV *Antea*, sta. AB1/4, 3°54'29.9"S 32°20'24.8"W to 3°53'19.3"S 32°19'26.3"W, 90 m, 2 Oct 2015, 14:00–14:30 h; NPM 5223, 1, 50 mm, RV *Antea*, sta. AB1/23, 5°08'36.7"S 34°42'48.5"W to 5°08'02.8"S 34°44'40.4"W, 35–100 m, 9 Oct 2015, 10:35–11:20 h.

MELANOCETIDAE

Females of the Melanocetidae are distinguished by having a short, deep body, globular; mouth large, opening oblique to nearly vertical; numerous well-developed teeth on jaws; vomer usually well-toothed, with a single row of up to 12 teeth; head smooth and rounded, spines absent on the sphenotic, quadrate and articular bones; illicium emerging on snout, its supporting pterygiophore fully embedded in skin of head; body smooth, dermal spines or spinules absent; dorsal fin long, with 13–16 (rarely 12 or 17) rays, anal fin short, with 4 (rarely 3 or 5) rays, and 15–23 pectoral-fin rays; males may attach temporarily to females (Pietsch, 2009).

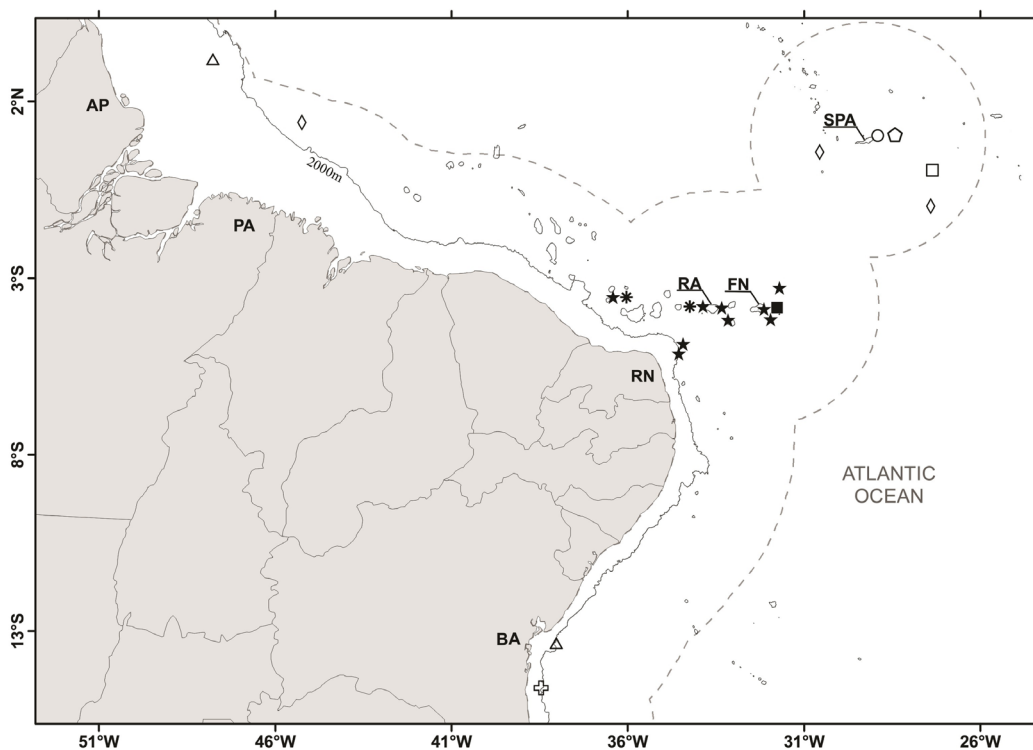


FIGURE 2 | Records of the Ceratiidae, Diceratiidae and Himantolophidae in Brazilian waters: *Ceratias uranoscopus* (square), *Ceratias holboelli* (cross), *Ceratias* sp. (asterisk), *Cryptopsaras couesii* (diamond), *Bufoceratias wedli* (triangle), *Himantolophus groenlandicus* (pentagon), *Himantolophus macroceras* (circle), *Himantolophus* sp. (star). Full symbols represent specimens collected during the ABRACOS surveys and open symbols are records from the literature (see text). Selected Brazilian States and islands are: AP – Amapá, PA – Pará, RN – Rio Grande do Norte, BA – Bahia; SPA – Saint Peter and Saint Paul Archipelago, FN – Fernando de Noronha Archipelago, RA – Rocas Atoll. Dashed line represents the outer limit of the Brazilian Exclusive Economic Zone.

Melanocetus Günther, 1864

Diagnosis. *Melanocetus* is the only genus in the Melanocetidae; diagnostic features are as those of the family (Pietsch, 2009).

Melanocetus johnsonii Günther, 1864

(Figs. 1C, 3)

Diagnosis. Metamorphosed females of *Melanocetus johnsonii* differ from congeners by the nearly straight anterior margin of the vomer; least outside width between frontals 13.5–28.6% SL; 48–134 teeth on upper jaw, 32–78 on lower jaw; length of longest tooth in lower jaw 8.4–25.0% SL; width of pectoral-fin lobe 10.7–17.8% SL; width of esca bulb 4.3–8.6% SL; length of illicium 32.4–60.8% SL; esca with posterior and usually anterior crests; skin with minute spinules over most of body; integument relatively thick (1.55 mm) (Pietsch, Van Duzer, 1980; Pietsch, 2009).

Geographical distribution. *Melanocetus johnsonii* occurs in the Atlantic, Pacific and Indian Oceans. It was previously reported in Brazilian waters based on specimens collected off Saint Peter and Saint Paul Archipelago (MCZ 42849, 0°24'N 27°32'W; Pietsch, Van Duzer, 1980), Espírito Santo State (MNRJ 30702, 20°27'40"S 39°38'06"W; MNRJ 30703, 19°43'40"S 38°39'50"W; Pietsch, 2009), and Trindade Island (ISH 2352–1968, 21°04'S 30°08'W; Pietsch, Van Duzer, 1980; Menezes *et al.*, 2003; Pietsch, 2009). The five specimens identified here were collected off Fernando de Noronha Archipelago and seamounts off Rio Grande do Norte State, between depths of 58 and 1,113 m (Fig. 3).

Remarks. Six additional juvenile (20–88 mm SL) specimens of *Melanocetus* collected in this study were only identified to genus (NPM 4956, NPM 4957, NPM 4967, NPM 4971, NPM 4976, NPM 4983). They were collected off Pernambuco State, Fernando de Noronha Archipelago, and near the seamounts off Rio Grande do Norte State, between depths of 680 and 1,113 m. *Melanocetus murrayi* Günther, 1887, with a circumglobal distribution, was recorded off Brazil, around Saint Peter and Saint Paul Archipelago (MCZ 42847, 1°20'30"S 27°37'30"W) and off northern Trindade Island (ISH 1180–1968, 17°33'S 28°13'W) (Pietsch, Van Duzer 1980; Menezes *et al.*, 2003; Pietsch, 2009; Melo *et al.*, 2020; Fig. 3).

Material examined. NPM 3837, 1, 10.5 mm, RV *Antea*, sta. AB1/7, 3°57'36.1"S 32°31'56.7"W to 3°56'48.1"S 32°31'05.3"W, 58 m, 3 Oct 2015, 19:22–19:52 h; NPM 3838, 1, 13.5 mm, RV *Antea*, sta. AB1/9, 3°28'15.4"S 32°45'31.5"W to 3°27'36.5"S 32°46'43.9"W, 105 m, 4 Oct 2015, 21:17–21:47 h; NPM 4970, 2, 14–19 mm (Fig. 1C), RV *Antea*, sta. AB2/52A, 3°43'16.2"S 33°25'09.8"W to 3°42'14.2"S 33°24'36.2"W, 822–984 m, 2 May 2017, 11:47–12:18 h; NPM 4981, 1, 17.5 mm, RV *Antea*, sta. AB2/59A, 3°38'01.6"S 36°31'46.3"W to 3°38'36.1"S 36°17'49.7"W, 700–1113 m, 5 May 2017, 21:57–22:37 h.

THAUMATICHTHYIDAE

Females of the Thaumaticthyidae are distinguished by having an elongate body; esca bearing 1–3 large toothlike denticles (bony hooks); upper jaw extending forward far beyond the lower jaw; premaxillae bearing numerous hooked teeth; upper arm of opercle divided into two or more branches; males and larvae of *Lasiognathus* are unknown, metamorphosed males of *Thaumaticthys* are unusually slender and elongate, apparently never parasitic on females (Pietsch, 2009).

Thaumaticthys sp.

(Figs. 1D, 3)

Diagnosis. Metamorphosed females of *Thaumaticthys* differ from those of *Lasiognathus*, the only other recognized genus of the family by having the body strongly depressed dorsoventrally (*vs.* body compressed laterally); a broad and also depressed head (*vs.* head narrow); pterygiophore of illicium short, completely hidden beneath skin of

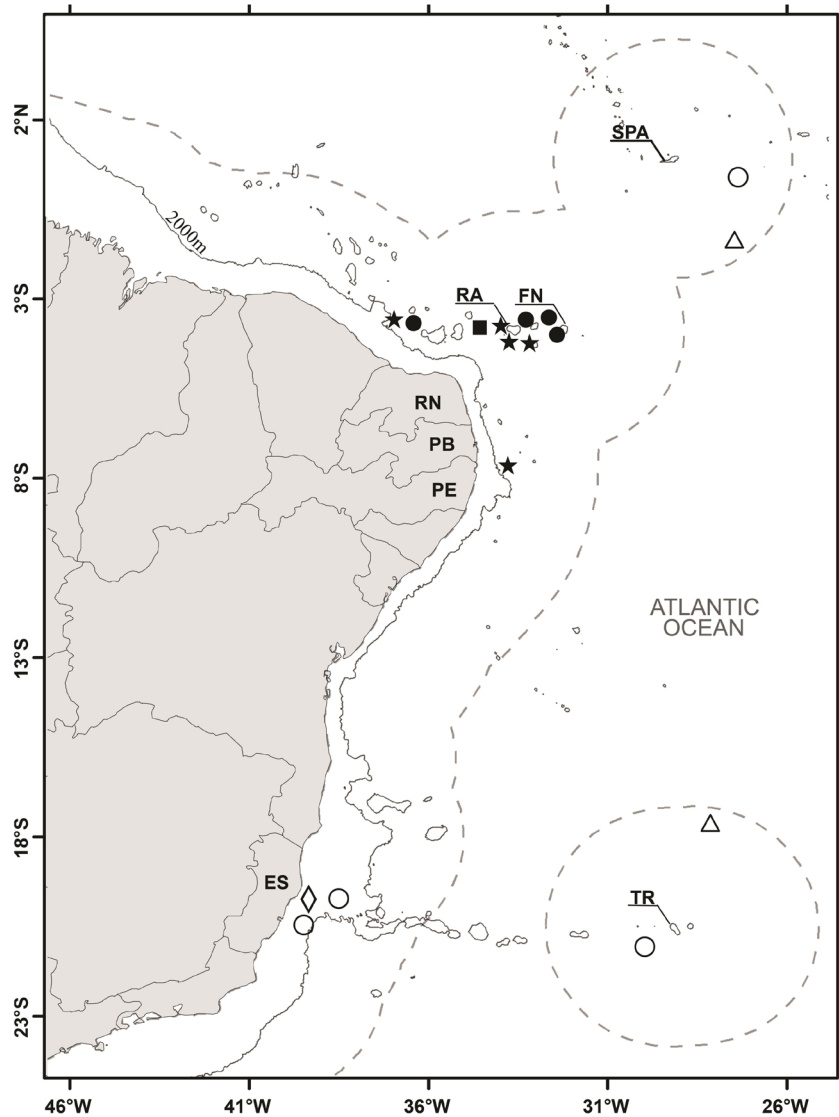


FIGURE 3 | Records of the Melanocetidae and Thaumatchthyidae in Brazilian waters: *Melanocetus johnsonii* (circle), *Melanocetus murrayi* (triangle), *Melanocetus* sp. (star), *Thaumatchthys binghami* (diamond), *Thaumatchthys* sp. (square). Full symbols represent specimens collected during the ABRACOS surveys and open symbols are records from the literature (see text). Selected Brazilian States and islands are: RN – Rio Grande do Norte, PB – Paraíba, PE – Pernambuco; ES – Espírito Santo; SPA – Saint Peter and Saint Paul Archipelago, FN – Fernando de Noronha Archipelago, RA – Rocas Atoll, TR – Trindade Island. Dashed line represents the outer limit of the Brazilian Exclusive Economic Zone.

head (*vs.* pterygiophore of illicium long, anterior tip emerging on snout from between frontal bones); illicium also short, embedded within the esca (*vs.* illicium long, greater than 35% SL); esca hanging from roof of mouth, bearing a single dermal denticle (*vs.* esca at the tip of illicium, with 2 or 3 large toothlike denticles); skin on ventral and lateral surfaces of head, body and tail covered with close-set dermal spinules (*vs.* skin naked, dermal spinules absent); 6 or 7 dorsal-fin rays (*vs.* 5), and 4 anal-fin rays (*vs.* 5) (Bertelsen, Struhsaker, 1977; Pietsch, 2009).

Geographical distribution. A single specimen collected at the seamounts off Rio Grande do Norte State, between depths of 830 and 1,030 m (Fig. 3).

Remarks. *Thaumatichthys* has three valid species, with only *Thaumatichthys binghami* Parr, 1927 reported from the western Atlantic, in the Bahamas, Gulf of Mexico, Caribbean Sea, and off Espírito Santo State, Brazil (MNRJ 30710, 19°45'S 39°30'W; Pietsch, 2009; Fig. 3). The single juvenile specimen recorded here could not be identified to species, but might be *T. binghami*.

Material examined. NPM 4985, 1, 32 mm (Fig. 1D), RV *Antea*, sta. AB2/54B, 3°45'17.2"S 34°41'04.0"W to 3°44'39.2"S 34°40'04.5"W, 830–1,030 m, mid-water trawl, 3 May 2017, 13:11–13:47 h.

ONEIRODIDAE

Females of the Oneirodidae are distinguished by having a short, deep to moderately elongate and laterally compressed body; mouth oblique to nearly horizontal, jaws equal anteriorly; illicium with a bulbous distal light organ; pterygiophore of the illicium usually emerging anteriorly on the snout, extending posteriorly on the back behind the head only in *Oneirodes*; top of head usually bearing sharp sphenotic spines, absent only in *Chaenophryne* and short in *Ctenochirichthys*; quadrate and articular spines usually well developed; skin smooth, dermal spines or spinules absent except in *Spiniphryne*; 4–8 dorsal-fin rays, 4–7 anal fin-rays, 13–30 pectoral-fin rays; a narrow, spatulate, anterodorsally directed process that overlaps the posterolateral surface of the respective sphenotic present in metamorphosed females; males usually free-living, non-parasitic, but two species apparently with facultative sexual parasitism (Pietsch, 2009).

In addition to the species reported below, three other oneirodids have been recorded in the Brazilian EEZ: *Microlophichthys microlophus* (Regan, 1925), collected off Saint Peter and Saint Paul Archipelago (MCZ 47566, 0°02'N 27°30'W to 0°03'N 27°31'W; MCZ 47567, 1°20'S 27°37'W; Pietsch, 2009); *Oneirodes notius* Pietsch, 1974, off Rio Grande do Sul State (MZUSP 78220, 31°04'S 49°15'W; Figueiredo *et al.*, 2002); and *Pentherichthys atratus* (Regan & Trewavas, 1932), collected off Fernando de Noronha Archipelago (MCZ 42852, 5°42'S 32°25'W; Pietsch, 2009) and Saint Peter and Saint Paul Archipelago (MCZ 47569, 1°20'S 27°37'W; MCZ 97115, 4°3'12"N 29°37'36"W; Pietsch, 2009) (Fig. 4).

Chaenophryne Regan, 1925

Diagnosis. Metamorphosed females of *Chaenophryne* differ from other genera of the Oneirodidae by the presence of blunt protuberances on the dorsal surface of the head, sphenotic spines absent (*vs.* protuberances absent and sphenotic spines present), opercle only slightly concave posteriorly (*vs.* opercle deeply notched posteriorly), pelvic bones triradiate to broadly expanded distally (*vs.* pelvic bones rod shaped, with or without slight distal expansions), bones, especially those closely associated with the external surface of the head, highly cancellous (*vs.* not cancellous in other ceratioids), and illicium pterygiophore long, 70–82% SL (*vs.* less than 50% SL) (Pietsch, 1974, 1975, 2009).

Chaenophryne draco Beebe, 1932

(Figs. 1E, 4)

Diagnosis. Among the five valid species of *Chaenophryne*, *C. draco*, *C. longiceps* Regan, 1925 and *C. ramifera* Regan & Trewavas, 1932 are reported from the Atlantic Ocean (Pietsch, 1975, 2009). Females of *Chaenophryne draco* differ from all other congeners by the absence of anterolateral esca appendages (*vs.* esca with 1–3 anterolateral appendages on each side), and ratio of number of teeth in upper and lower jaws in specimens 20 mm or larger (1.08–1.45 *vs.* 0.76–1.30). The species is further distinguished from *C. longiceps* by having esca with an unpaired internally pigmented anterior appendage (*vs.* esca with a pair of internally pigmented anterior appendages); width of esca bulb 2.1–6.6% SL in specimens larger than 20 mm (*vs.* width of esca bulb 5.3–11.4% SL in specimens larger than 20 mm); pectoral-fin rays 16–19, rarely more than 18 (*vs.* 17–22, rarely less than 18). *Chaenophryne draco* also seems to differ from *C. ramifera* by a slightly shorter illicium (24.0–36.4% SL *vs.* 32.8–47.4% SL) and by fewer dorsal-fin rays (6–8 *vs.* 7–8) (Pietsch, 1975; Pietsch, 2007, 2009).

Geographical distribution. *Chaenophryne draco* is widespread in the Atlantic, Indian, and Pacific Oceans. In the Atlantic, it has been reported from Greenland to Cape Verde, with additional records from off Cape Town, South Africa, and off Espírito Santo State, Brazil (MNRJ 30707, 19°43'40"S 38°39'50"W; Pietsch, 1975, 2009; Sutton *et al.*, 2008; Porteiro *et al.*, 2017). Species is reported here based on two specimens collected off Pernambuco State and Rocas Atoll, between depths of 680 and 984 m (Fig. 4).

Material examined. NPM 4954, 1, 90 mm (Fig. 1E), RV *Antea*, sta. AB2/16, 7°36'15.0"S 33°59'30.0"W to 7°36'49.3"S 33°57'18.7"W, 680 m, 14 Apr 2017, 21:53–22:39 h; NPM 4969, 1, 55 mm, RV *Antea*, sta. AB2/52A, 3°43'16.2"S 33°25'09.8"W to 3°42'14.2"S 33°24'36.2"W, 822–984 m, 2 May 2017, 11:47–12:18 h.

Chaenophryne ramifera Regan & Trewavas, 1932

(Figs. 1F, 4)

Diagnosis. Females of *Chaenophryne ramifera* are distinguished from those of *C. longiceps* by having a single, elongate, internally pigmented, anterior esca appendage (*vs.* esca with a pair of internally pigmented, anterior appendages), medial esca appendages absent (*vs.* medial esca appendage or appendages present), width of esca bulb 4.5–6.5% SL in specimens 20 mm or larger (*vs.* 5.3–11.4% SL in specimens 20 mm or larger), pectoral-fin rays 16–19 (*vs.* 17–22, rarely less than 18); they are also distinguished from *C. draco* by having two or three filamentous, anterolateral esca appendages on each side (*vs.* esca without anterolateral appendages), and by the ratio between number of teeth in upper jaw to number of teeth in lower jaw 0.76–0.98 (*vs.* 1.08–1.45) (Pietsch, 1975, 2007, 2009).

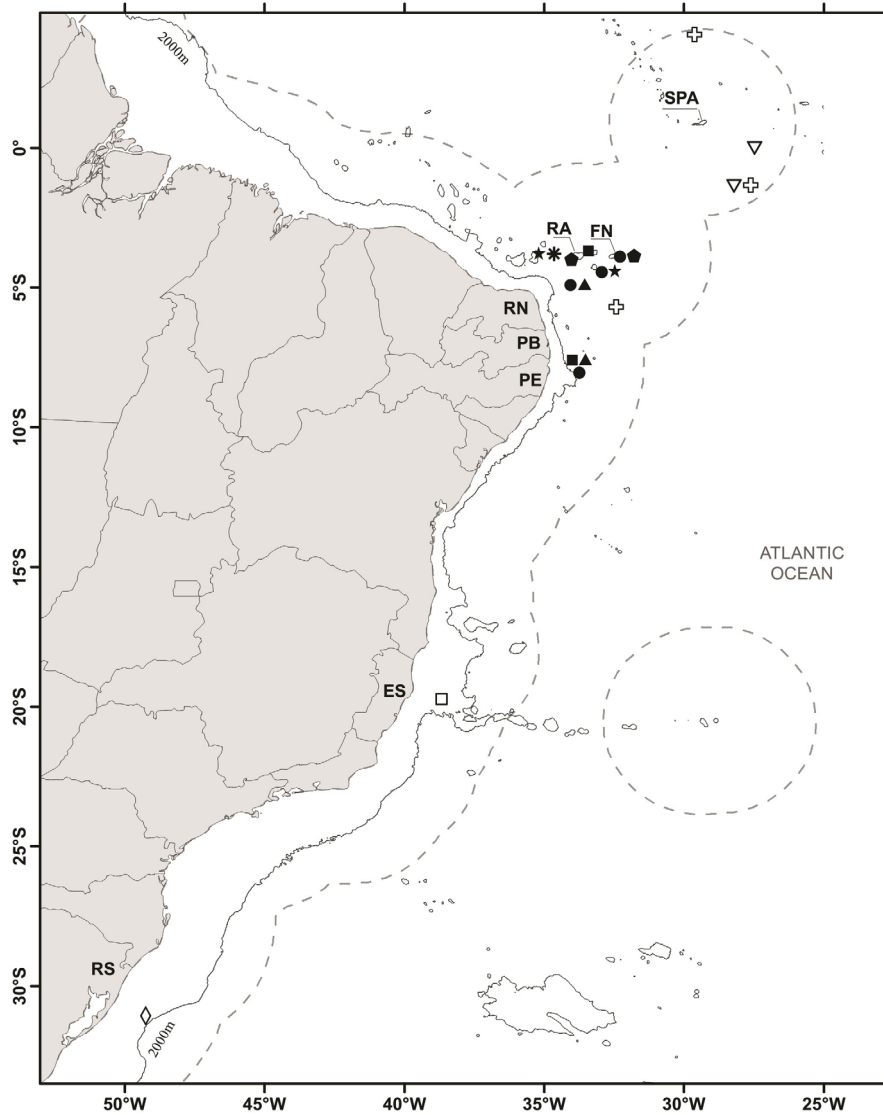


FIGURE 4 | Records of the Oneirodidae in Brazilian waters: *Chaenophryne draco* (square), *Chaenophryne ramifera* (circle), *Chaenophryne* sp. (pentagon), *Dolopichthys* sp. (asterisk), *Microlophichthys microlophus* (upside-down triangle), *Oneirodes anisacanthus* (star), *Oneirodes carlsbergi* (triangle), *Oneirodes notius* (diamond), *Pentherichthys atratus* (cross). Full symbols represent specimens collected during the ABRACOS surveys and open symbols are records from the literature (see text). Selected Brazilian States and islands are: RN – Rio Grande do Norte, PB – Paraíba, PE – Pernambuco; ES – Espírito Santo, RS – Rio Grande do Sul; SPA – Saint Peter and Saint Paul Archipelago, FN – Fernando de Noronha Archipelago, RA – Rocas Atoll. Dashed line represents the outer limit of the Brazilian Exclusive Economic Zone.

Geographical distribution. *Chaenophryne ramifera* occurs in the Atlantic, Indian and Pacific Oceans. In the Atlantic, the species has been reported between 35°N off North Carolina and 12°S off Angola, with records near the Brazilian EEZ off Saint Peter and Saint Paul Archipelago (Pietsch, 1975, 2009). *Chaenophryne ramifera* is recorded for the first time in the Brazilian EEZ based on specimens collected off Fernando de Noronha Archipelago, Rocas Atoll, and Rio Grande do Norte and Pernambuco States, between depths of 505 and 850 m (Fig. 4).

Remarks. Two other specimens of *Chaenophryne* (NPM 4963, 28 mm SL; NPM 5219, 17 mm SL) could not be identified to species due to their extremely small sizes. They were collected from off Fernando de Noronha Archipelago and Rocas Atoll, between depths of 510 and 850 m (Fig. 4).

Material examined. NPM 4955, 1, 32 mm (Fig. 1F), RV *Antea*, sta. AB2/16, 7°36'15.0"S 33°59'30.0"W to 7°36'49.3"S 33°57'18.7"W, 680 m, 14 Apr 2017, 21:53–22:39 h; NPM 4958, 1, 40 mm, RV *Antea*, sta. AB2/39, 4°52'26.9"S 34°03'32.3"W to 4°50'52.8"S 34°05'06.5"W, 650–800 m, 24 Apr 2017, 21:49–22:37 h; NPM 5061, 1, 44 mm, RV *Antea*, sta. AB2/44A, 3°52'52.5"S 32°17'33.3"W to 3°52'13.4"S 32°16'28.0"W, 850 m, 28 Apr 2017, 12:44–13:17 h; NPM 5062, 1, 50 mm, RV *Antea*, sta. AB2/48A, 4°25'05.3"S 32°57'52.1"W to 4°25'24.9"S 32°56'55.5"W, 505 m, 30 Apr 2017, 10:30–10:58 h.

Dolopichthys Garman, 1899

Diagnosis. Females of *Dolopichthys* differ from those of *Chaenophryne* by the presence of sphenotic spines (*vs.* absence of sphenotic spines), opercle deeply notched posteriorly (*vs.* opercle not deeply notched posteriorly), pelvic bones rod shaped, with or without slight distal expansion (*vs.* pelvic bones triradiate or greatly expanded distally); from *Oneirodes*, *Tyrannophryne*, *Phyllorhinichthys*, *Microlophichthys*, and *Danaphryne* by having the dorsal margin of frontal bones nearly straight (*vs.* dorsal margin of frontal bones strongly convex) and subopercle long and narrow, ventral end strongly oval (*vs.* subopercle short and broad, ventral end nearly circular); from *Ctenochirichthys*, *Leptacanthichthys*, *Chirophryne* and *Puck* by the pectoral-fin lobe broad, shorter than the longest pectoral-fin rays (*vs.* pectoral-fin lobe narrow, longer than longest pectoral-fin rays); from *Bertella* by having the hyomandibula with a double head (*vs.* hyomandibula with a single head); from *Dermatias* by the depth of caudal peduncle less than 20% SL (*vs.* greater than 20% SL); from *Lophodolos* by the illicial apparatus emerging near the tip of snout, between the frontal bones (*vs.* illicial apparatus emerging from the dorsal surface of head, between or behind sphenotic spines); from *Pentherichthys* by having the lower jaw with a symphyseal spine (*vs.* lower jaw without a symphyseal spine, ventral margin of dentaries at symphysis concave), and caudal-fin rays without internal pigment (*vs.* caudal-fin rays internally pigmented); and from *Spiniphryne* by the skin naked or the presence of only minute, widely spaced dermal spinules, visible only with the aid of a microscope in cleared and stained specimens (*vs.* skin covered with close-set dermal spinules) (Pietsch, 2009).

Dolopichthys sp.

(Figs. 1G, 4)

Diagnosis. As for genus.

Geographical distribution. All seven valid species of *Dolopichthys* occur in the Atlantic Ocean and two of them were reported from the western South Atlantic near

the Brazilian EEZ: *Dolopichthys danae* Regan, 1926, and *D. pullatus* Regan & Trewavas, 1932 (Pietsch, 1972, 2009). The small specimen of *Dolopichthys* reported here and identified only to genus, however, represents the first record of the genus in Brazilian waters. The specimen was collected near the seamounts off Rio Grande do Norte State, between depths of 830 and 1,030 m (Fig. 4).

Material examined. NPM 4980, 1, 35 mm (Fig. 1G), RV *Antea*, sta. AB2/54B, 3°45'17.2"S 34°41'04.0"W to 3°44'39.2"S 34°40'04.5"W, 830–1,030 m, 3 May 2017, 13:11–13:47 h.

Oneirodes Lütken, 1871

Diagnosis. *Oneirodes* is the largest genus of the Ceratioidei, with 35 currently recognized species. Metamorphosed females of *Oneirodes* differ from those of all other genera of the Oneirodidae by having the posterior end of the pterygiophore of the illicium protruding from the dorsal midline of the trunk behind the head (*vs.* posterior end of the pterygiophore of the illicium not protruding from the dorsal midline of the trunk behind the head) (Pietsch, 2009).

Oneirodes anisacanthus Regan, 1925

(Figs. 1H, 4)

Diagnosis. Females of *Oneirodes anisacanthus* differ from those of its congeners, except *O. placionema*, *O. krefftii*, *O. posti*, *O. rosenblatti*, *O. dicromischus*, *O. luetkeni*, *O. carlsbergi*, and those of the *O. schmidti* group, by the presence of a well-developed lateral esca appendage (*vs.* esca with lateral appendage minute or absent). *Oneirodes anisacanthus* differs from *O. placionema* by the posterior esca appendage about one-third the length of esca bulb (*vs.* posterior esca appendage minute), anterior appendage anterodorsally directed, bearing numerous short filaments, and 2 unpigmented tapering filaments on anterior margin near the distal tip (*vs.* anterior appendage narrow, elongate, and anteroventrally directed, bearing a single short distal filament); from *O. krefftii* and *O. posti* by the esca without elongate medial appendages (*vs.* esca with 2 or 3 medial filaments more than twice the length of esca bulb); from *O. rosenblatti* and *O. dicromischus* by the lower jaw with fewer than 90 teeth in specimens greater than 45 mm, fewer than 60 teeth in specimens greater than 25 mm (*vs.* lower jaw with more than 90 teeth in specimens greater than 45 mm, more than 60 teeth in specimens greater than 25 mm), 3–9 (usually fewer than 8) teeth on vomer in specimens greater than 25 mm (*vs.* 8–14, usually more than 9 teeth); from *O. luetkeni* and *O. carlsbergi* by the presence of teeth on the epibranchial of the first gill arch (*vs.* epibranchial teeth absent); and from species of the *O. schmidti* group by the anterior esca appendage internally pigmented, anterolateral appendages absent (*vs.* anterior appendage without internal pigment, usually two pairs of filamentous anterolateral appendages) (Pietsch, 1974, 2009; Orr, 1991; Prokofiev, 2014a,b; Ho *et al.*, 2016; Rajeeshkumar *et al.*, 2017; Ho, Shao, 2019).

Geographical distribution. *Oneirodes anisacanthus* is widespread in the Atlantic Ocean, with records from off eastern Greenland, the Caribbean Sea, Madeira, Gulf of Guinea, and off Cape Town, South Africa (Pietsch, 1974, 2009). The two specimens collected around the Fernando de Noronha Archipelago and the seamounts off Rio Grande do Norte State, between depths of 505 and 1,030 m (Fig. 4), represent the first record of the species in Brazilian waters and in the western South Atlantic.

Material examined. NPM 4965, 1, 48 mm, RV *Antea*, sta. AB2/48A, 4°25'05.3"S 32°57'52.1"W to 4°25'24.9"S 32°56'55.5"W, 505 m, 30 Apr 2017, 10:30–10:58 h; NPM 4977, 1, 30 mm (Fig. 1H), RV *Antea*, sta. AB2/54B, 3°45'17.2"S 34°41'04.0"W to 3°44'39.2"S 34°40'04.5"W, 830–1,030 m, 3 May 2017, 13:11–13:47 h.

Oneirodes carlsbergi (Regan & Trewavas, 1932)

(Figs. 1I, 4)

Diagnosis. *Oneirodes carlsbergi* differs from its congeners, except *O. luetkeni*, by the presence of teeth on the epibranchial of the first gill arch (*vs.* teeth absent). It differs from *O. luetkeni*, reported only from the eastern Pacific, by the number of teeth on the epibranchial of the first gill arch (1–5 *vs.* 6–17), number of toothed pharyngobranchials (two pairs of tooth-bearing pharyngobranchials *vs.* a single pair of tooth-bearing pharyngobranchials), ratio of lengths of dorsal and ventral forks of opercle (0.51–0.61 *vs.* 0.60–0.71), and esca with a tapering and internally pigmented anterior appendage (*vs.* anterior appendage without internal pigment, anterolateral appendage represented by a broad membranous flap) (Pietsch, 1974, 2009; Orr, 1991; Prokofiev, 2014a,b; Ho *et al.*, 2016; Rajeeshkumar *et al.*, 2017; Ho, Shao, 2019).

Geographical distribution. *Oneirodes carlsbergi* seems to have a circumtropical distribution between approximately 18°N and 8°S (Pietsch, 2009; Ho *et al.*, 2016; Ho, Shao, 2019). One specimen recorded far from this presumably circumtropical range was collected off the Irish Atlantic slope (Pietsch, 2009). Other records in the Atlantic Ocean range from 17°49'N to 5°34'S, and include two records near the Brazilian EEZ (ISH 660/66, 5°34'S 26°58'W; ISH 924/68, 3°00'S 26°16'W) (Pietsch, 1974, 2009). In the present study *O. carlsbergi* is reported for the first time in Brazilian waters based on two specimens collected off Pernambuco State and Rocas Atoll, between depths of 650 and 800 m (Fig. 4).

Material examined. NPM 4953, 1, 98 mm (Fig. 1I), RV *Antea*, sta. AB2/16, 7°36'15.0"S 33°59'30.0"W to 7°36'49.3"S 33°57'18.7"W, 680 m, 14 Apr 2017, 21:53–22:39 h; NPM 4960, 1, 18.5 mm, RV *Antea*, sta. AB2/39, 4°52'26.9"S 34°03'32.3"W to 4°50'52.8"S 34°05'06.5"W, 650–800 m, 24 Apr 2017, 21:49–22:37 h.

CAULOPHYRIDAE

Females of the Caulophrynidae are distinguished by having a short, deep body, more or less globular; mouth large, lower jaw usually extending posteriorly beyond the base

of the pectoral-fin lobe; jaw teeth unusually large; epibranchial and ceratobranchial teeth absent; illicium without a bulbous bacteria-filled light organ, the pterygiophore of the illicium fully embedded beneath skin of head; skin smooth and naked, spines or dermal denticles absent; lateral-line structures unusually well-developed, sense organs at the tips of cutaneous papillae; dorsal- and anal-fin rays apparently free, not interconnected by membrane, and usually longer than 60% SL; and 8 caudal-fin rays. Larvae of the Caulophrynidae are also distinguished in the Ceratioidei by the presence of pelvic fins, which are absent at all stages in other families of the suborder. Males are probably facultative parasites on females (Pietsch, 2009).

Caulophryne Goode & Bean, 1896

Diagnosis. Metamorphosed females of *Caulophryne* can be distinguished from those of *Robia*, the only other genus of the family (known from a single, 41 mm SL female collected in the western Central Pacific), by having a considerably shorter illicium (less than 130 mm *vs.* about 270 mm) and by the number and size of dorsal- and anal-fin rays (14–22 dorsal-fin rays, the longest ray > 70% SL *vs.* 6 dorsal-fin rays, the longest ray < 65% SL; 12–19 anal-fin rays, the longest ray > 60% SL *vs.* 5 anal-fin rays, the longest ray < 40% SL) (Pietsch, 2009).

Caulophryne sp.

(Figs. 1J, 5)

Diagnosis. Same as for genus.

Geographical distribution. Species of *Caulophryne* have been reported from the Atlantic, Indian and Pacific Oceans between approximately 65°N and 50°S (Pietsch, 2009). Three of the four currently recognized species of the genus are known from the Atlantic Ocean: *Caulophryne jordani* Goode & Bean, 1896, known from the North Atlantic up to about 5°N; *Caulophryne pelagica* (Brauer, 1902), recorded in the Atlantic at a single locality off Cape Verde Islands; and *Caulophryne polynema* Regan, 1930, recorded in the North and South Atlantic to 28°S off Africa, with no records in the western South Atlantic (Pietsch, 1979, 2009). The extremely small specimen of *Caulophryne* sp. reported here was collected off Rio Grande do Norte State, between depths of 35 and 100 m, and represents the first record of the genus in Brazilian waters and in the western South Atlantic (Fig. 5).

Material examined. NPM 3835, 1, 6 mm SL (Fig. 1J), RV *Antea*, sta. AB1/23, 5°08'36.7"S 34°42'48.5"W to 5°08'02.8"S 34°44'40.4"W, 35–100 m, 9 Oct 2015, 10:35–11:20 h.

GIGANTACTINIDAE

Females of the Gigantactinidae are distinguished by having an elongate, laterally compressed body; a long slender illicium, with highly variable lengths (less than SL to

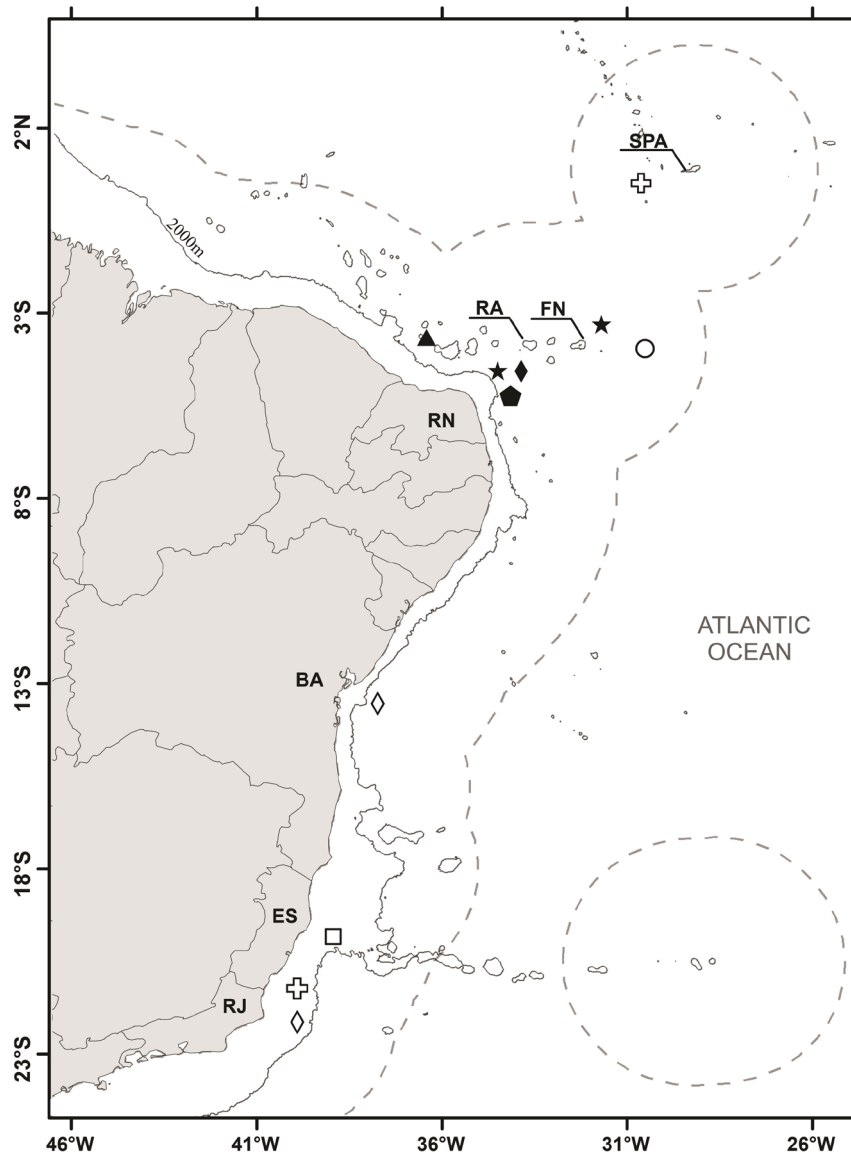


FIGURE 5 | Records of the Caulophrynidae, Gigantactinidae, and Linophrynidae in Brazilian waters: *Caulophryne* sp. (pentagon), *Gigantactis longicirra* (square), *Gigantactis vanhoeffeni* (cross), *Gigantactis watermani* (triangle), *Gigantactis* sp. (diamond), *Rhynchactis* sp. (star), *Linophryne arborifera* (circle). Full symbols represent specimens collected during the ABRACOS surveys and open symbols are records from the literature (see text). Selected Brazilian States and oceanic islands are RN – Rio Grande do Norte, BA – Bahia, ES – Espírito Santo, RJ – Rio de Janeiro; SPA – Saint Peter and Saint Paul Archipelago, FN – Fernando de Noronha Archipelago, RA – Rocas Atoll. Dashed line represents the outer limit of the Brazilian Exclusive Economic Zone.

nearly five times SL) emerging from the anteriormost tip of the snout; length of head less than 35% SL; mouth nearly horizontal, upper jaw extending slightly beyond lower jaw; epibranchial and ceratobranchial teeth absent; caudal peduncle unusually long and slender, more than 20% SL; 3–10 dorsal-fin rays, 3–8 anal-fin rays; caudal fin usually incised posteriorly, 9 caudal-fin rays, usually highly elongate. Males are probably free living, never parasitic (Pietsch, 2009).

In addition to the species recorded here, two species of the family have been previously reported in Brazilian waters: *Gigantactis longicirra* Waterman, 1939 and *G. vanhoeffeni* Brauer, 1902. *Gigantactis longicirra* is known from the Atlantic and Pacific Oceans. In the Atlantic, it occurs in the Gulf of Saint Lawrence, Canada, south along the New England slope to the Gulf of Mexico, Caribbean Sea, off Venezuela, and in the Gulf of Guinea. A single specimen was also collected off Espírito Santo State, Brazil (MNRJ 30700, 19°48'29"S 39°02'21"W; Pietsch, 2009). *Gigantactis vanhoeffeni* is known from the Atlantic, Indian and Pacific Oceans, with records in the Atlantic ranging from off western Greenland to the South Atlantic, including the Gulf of Mexico, Caribbean Sea, Cape Verde Islands, Gulf of Guinea, and off South Africa (Bertelsen *et al.*, 1981; Sutton *et al.*, 2008; Pietsch, 2009; Porteiro *et al.*, 2017). In Brazil, *G. vanhoeffeni* was recorded based on specimens collected off Saint Peter and Saint Paul Archipelago (MCZ 61049, 0°34'N 30°43'W) and off Espírito Santo State (MNRJ 30708, 21°12'18"S 40°00'53"W; Costa *et al.*, 2007; Pietsch, 2009; Mincarone *et al.*, 2017; Melo *et al.*, 2020: 188, as “*verhoeffeni*”) (Fig. 5).

Two additional records of *Gigantactis* sp. in Brazilian waters are also known, one consisting of a female collected off Bahia State (MNRJ 30699, 13°30'28"S 38°38'59"W; Costa *et al.*, 2007), and a female larva, collected off Rio de Janeiro State (DZUFRJ 1286, 22°06'52.3"S 39°48'46.2"W; Bonecker *et al.*, 2014) (Fig. 5).

Gigantactis Brauer, 1902

Diagnosis. Metamorphosed females of *Gigantactis* are distinguished from those of *Rhynchactis*, the other genus of the family, by the absence of pelvic bones and by having 5–9 dorsal-fin rays (rarely 4–10) and 4–7 anal-fin rays (rarely 8) (*vs.* 3–4 dorsal-fin rays, rarely 5, and 3–4 anal-fin rays). They further differ from those of *Rhynchactis* by the following characters: frontal and parietal bones present (*vs.* absent), premaxilla well developed, with teeth present throughout their length (*vs.* premaxilla represented by a remnant bearing 0–2 teeth), maxilla reduced to threadlike remnants (*vs.* maxillae absent), dentary with several rows of strong recurved teeth (*vs.* dentary toothless or with only minute teeth), a single hypohyal (*vs.* two hypohyals), all caudal-fin rays unbranched (*vs.* 9 caudal-fin rays, 2 simple + 4 branched + 3 simple), skin spinulose (*vs.* skin covered with minute spinules in larger specimens, but juveniles naked), snout produced in front of mouth, illicium originating at its tip (*vs.* snout truncated, illicium origin slightly behind its tip), and esca consisting of an expanded luminous bulb (*vs.* absence of bulbous, terminal, esca light organs) (Bertelsen *et al.*, 1981; Pietsch, 2009).

Gigantactis watermani Bertelsen, Pietsch & Lavenberg, 1981

(Figs. 5, 6A, 7)

Diagnosis. Twenty species of *Gigantactis* are recognized (two of doubtful validity: *G. ovifer* Regan & Trewavas, 1932 and *G. filibulbosus* Fraser-Brunner, 1935), of which 14 are reported for the Atlantic. *Gigantactis watermani* differs from *G. elsmanni*, *G. krefftii*, and *G. perlatus* by the length of the illicium (130–490% SL, rarely less than 200%, *vs.* 60–120% SL); from *G. golovani*, *G. macronema*, and *G. gargantua* (North Pacific and

eastern South Indian Ocean) by the esca filaments (distal esca filaments simple, without posterior filaments on or below its base *vs.* esca with distal filaments branched, several filaments emerging from and below its base); it further differs from *G. gargantua* by the pigmentation of distal esca filaments (heavily pigmented for more than one-half their length *vs.* lightly pigmented for less than one-fifth their length) and position of proximal esca filaments (restricted to the anterior margin of the esca bulb *vs.* not restricted to the anterior margin of esca bulb); from *G. ios*, *G. longicauda*, *G. macronema*, *G. microdontis* (eastern Pacific), and *G. savagei* (eastern North Pacific) by the presence of a group of anterior filaments arising from the base of esca (*vs.* absence), esca bulb structure (distal part of esca bulb bearing four or five pairs of stout filaments along posterior margin *vs.* filaments of distal part of esca bulb different from above), and length of caudal-fin rays (second and seventh greater than 50% SL *vs.* longest caudal-fin rays less than 40% SL); from *G. herwigi* by the number of filaments at esca base (10 *vs.* less than 10), number of pair of filaments on the distal part of esca bulb (four or five, each with a pigmented swollen base *vs.* four, each gradually tapering and only faintly pigmented at base); from *G. longicirra* by the number and length of the dorsal-fin rays (4–7, all about equal in length *vs.* 8–10, the first and last distinctly longer than intermediate rays) and length of the first and eighth caudal-fin rays (less than 40% *vs.* 60–100% SL); and from *G. gibbsi*, *G. gracilicauda*, *G. meadi*, *G. vanhoeffeni*, and *G. paxtoni* (western South Indian Ocean and western South Pacific) by the absence of a darkly pigmented, spinulose distal prolongation in the esca (*vs.* presence of dark pigment) (Pietsch, 2009).



FIGURE 6 | Species of the Gigantactinidae reported in this study: **A.** *Gigantactis watermani*, NPM 4424, 170 mm SL; **B.** *Rhynchactis* sp., NPM 4425, 113 mm SL. Scale bars = 10 mm.

Geographical distribution. Only two metamorphosed females of *Gigantactis watermani* were previously known, one from the eastern Tropical Atlantic (ISH 2330/71, 1°04'N 18°22'W) and another from the western Tropical Pacific, off New Caledonia (Pietsch, 2009). The specimen collected off seamounts of Rio Grande do Norte State, between depths of 700 and 1,113 m, represents the third known female specimen of the species and the first record in the South Atlantic (Fig. 5).

Remarks. Morphological and meristic data of the specimen agree with the description provided by Bertelsen *et al.* (1981) for the holotype, but some slightly differences were noted in its esca anatomy. The esca is bilaterally asymmetric, with four stout, tapering filaments present on the left side and five filaments present on the right side. The base of the most proximal filament of the right side is, however, reduced, with the structure mostly represented by the swollen, dark pigmented proximal part and a tiny unpigmented narrow tip (Fig. 7). In addition, the left filament of the most distal pair of filaments is secondarily branched, resulting in three filaments for this pair. In the holotype, the filaments of the most distal pair have a single branch. Bertelsen *et al.* (1981) also indicated the presence of 12 narrow unpigmented filaments on the anterior margin base of the esca bulb, but 14 filaments are present in the specimen examined (Fig. 7), a number that is within the range noted by Pietsch (2009: 467) for the species.

One additional small-sized specimen (NPM 3836, 6 mm SL) of *Gigantactis* collected off Rio Grande do Norte State, between depths of 35 and 100 m, was identified only to genus (Fig. 5).

Material examined. NPM 4424, 1, 170 mm (Fig. 6A), RV *Antea*, sta. AB2/59A, 3°38'01.6"S 36°31'46.3"W to 3°38'36.1"S 36°17'49.7"W, 700–1,113 m, 5 May 2017, 21:57–22:37 h.

Rhynchactis Regan, 1925

Diagnosis. See “Diagnosis” of *Gigantactis*.

Rhynchactis sp.

(Figs. 5, 6B)

Geographical distribution. Two specimens were collected off Rio Grande do Norte State and Fernando de Noronha Archipelago between depths of 650 and 800 m (Fig. 5). As discussed below, they could not be identified to species, but represent the first record of the genus in Brazilian waters.

Remarks. Of the three valid species of *Rhynchactis*, two occur in the Atlantic: *Rhynchactis leptonema* Regan, 1925 and *Rhynchactis macrothrix* Bertelsen & Pietsch, 1998 (Pietsch, 2009). Both species are poorly represented in collections and their geographic distributions are poorly known (Pietsch, 2009). *Rhynchactis leptonema* has been collected in a few localities of the Atlantic and Pacific (off Hawaii and Taiwan). In the Atlantic, it is known from the holotype collected in the western Tropical Atlantic (ZMUC P92133,

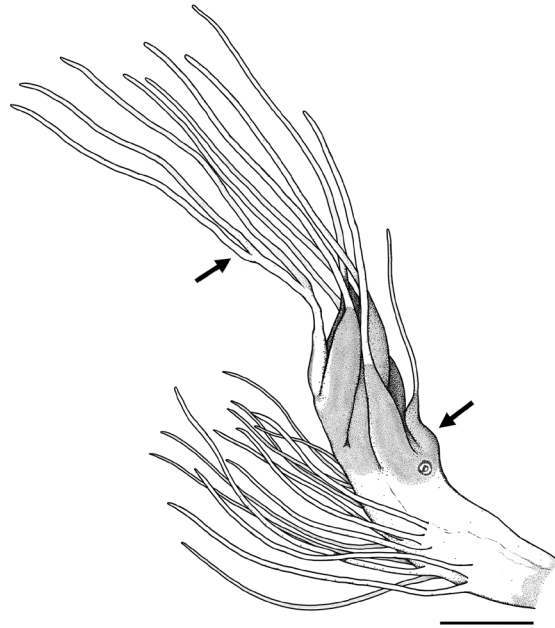


FIGURE 7 | Esca of *Gigantactis watermani*, NPM 4424, in left ventrolateral view. Arrows indicate the secondary branching of the left filament of the most distal pair of filaments (upper left) and the reduced base of the most proximal filament of the right side (lower right). Scale bar = 5 mm.

8°19'N 44°35'W). *Rhynchactis macrothrix* is also known from widely spread localities in the Atlantic and the western Indian and western Pacific Oceans. In the Atlantic, it is known from three specimens: the holotype collected in central equatorial waters (ISH 605/74, 7°55'N 32°41'W), and two specimens collected off Bermuda and in the Gulf of Mexico (Bertelsen, Pietsch, 1998; Pietsch, 2009).

The larger specimen reported here (NPM 4425, 113 mm SL; Fig. 6B) is in overall good condition but while it retains the full length of the illicium, the skin of the structure has been lost. The illicium length (208% SL) clearly indicates that it is not *R. leptonema* (maximum 177% SL; Bertelsen *et al.*, 1981), being more similar in that respect to *R. microthrix* (210% SL; Bertelsen, Pietsch, 1998). The smaller specimen (NPM 5014) is an unidentified juvenile.

Material examined. NPM 4425, 1, 113 mm (Fig. 6B), RV *Antea*, sta. AB2/42A, 3°15'28.1"S 31°48'29.1"W to 3°15'27.8"S 31°50'40.6"W, 780 m, 27 Apr 2017, 12:23–12:26 h; NPM 5014, 1, 42 mm, RV *Antea*, sta. AB2/39, 4°52'26.9"S 34°35'22.9"W to 4°50'52.8"S 34°51'04.7"W, 650–800 m, 24 Apr 2017, 21:49–22:37 h.

DISCUSSION

Nine of the 11 families of the Ceratioidei are confirmed in Brazilian waters, with four species (*Chaenophryne ramifera*, *Gigantactis watermani*, *Oneirodes anisacanthus*, and *O. carlsbergi*) and three genera (*Caulophryne*, *Dolopichthys*, and *Rhynchactis*) reported here for the first time. Three other species (*Ceratias uranoscopus*, *Chaenophryne draco*, and *Melanocetus johnsonii*) have their distributions extended in the Brazilian Exclusive Economic Zone.

Species of other ceratioid families previously recorded in Brazilian waters but not collected in the ABRACOS expeditions are *Bufoceratias wedli* (Pietschmann, 1926) (Diceratiidae), and *Linophryne arborifera* Regan, 1925 (Linophrynidae). *Bufoceratias wedli* is widely distributed along the eastern and western coasts of the Atlantic Ocean. It was listed by Asano Filho *et al.* (2005) among other fishes trawled off Amapá State, without reporting voucher specimens. Based on that report, Klautau *et al.* (2020) recently included the species in their inventory of the deep-sea teleosts of the Brazilian north coast. Three additional specimens of *Bufoceratias wedli* were subsequently reported off Salvador, Bahia State (MNRJ 30705, 13°19'57"S 38°19'39"W; MNRJ 30706, 13°21'50"S 38°16'41"W; MNRJ 30709, 13°17'35"S 38°17'36"W; Costa *et al.*, 2007; Pietsch, 2009); Fig. 2. *Linophryne arborifera* was reported in Brazilian waters based on a specimen collected off eastern Fernando de Noronha Archipelago (MCZ 44171, 3°55'S 30°38'W; Bertelsen, 1980); Fig. 5. Melo *et al.* (2020: 188) also included *Himantolophus paucifilosus* (Himantolophidae) and *Neoceratias spinifer* Pappenheim, 1914 (Neoceratiidae) in their list of the deep-sea fishes off Brazil. The record of *H. paucifilosus* was based on paratypes and other specimens collected in international waters off northern South America in the vicinities of the Brazilian EEZ (ZMH 138226, 1°N 26°W; ZMH 138231, 2°N 35°W; ISH 640–1974, 2°30'N 34°52'W; Pietsch, 2009). That is also the case for *Neoceratias spinifer*, known from only two records in the South Atlantic, one near the Brazilian EEZ (MCZ 51292, 10°20'31"N 30°32'31"W; Pietsch, 2009). Both species therefore probably occur in Brazilian waters, but have not yet been recorded in the country's EEZ.

Summing up, a total of 23 species of the Ceratioidei, across 15 genera and nine families, occur in the Brazilian Exclusive Economic Zone (Tab. 1). Most of those species were reported along the northeastern coast and off oceanic islands. Given that most of the Brazilian coast has not been sufficiently explored in terms of its deep-sea fauna, these numbers are certainly an underestimate, reinforcing the need for more deep-water surveys in the Brazilian EEZ and in the western South Atlantic overall. Exploring deeper waters and trawling for longer distances will certainly result in an increase in the number of deep-water fishes known from the region.

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TABLE 1 | Confirmed records of the Ceratioidei in the Brazilian Exclusive Economic Zone. Asterisk indicates records based on larval and/or small juvenile specimens only.

Species	Distribution	References
Ceratiidae		
<i>Ceratias holboelli</i> Krøyer, 1845	Circumglobal	Pietsch (2009); Melo <i>et al.</i> (2020)
<i>Ceratias uranoscopus</i> Murray, 1877	Circumglobal	Pietsch (1986); Menezes <i>et al.</i> (2003); Melo <i>et al.</i> (2020); this study
<i>Cryptosaras couesii</i> Gill, 1883	Circumglobal	Pietsch (1986); Menezes <i>et al.</i> (2003); Melo <i>et al.</i> (2020)
Himantolophidae		
<i>Himantolophus groenlandicus</i> Reinhardt, 1837	Atlantic and probably Indian and Pacific	Bertelsen, Krefft (1988); Melo <i>et al.</i> (2020)
<i>Himantolophus macroceras</i> Bertelsen & Krefft, 1988	Atlantic	Bertelsen, Krefft (1988); Melo <i>et al.</i> (2020)
Diceratiidae		
<i>Bufoceratias wedli</i> (Pietschmann, 1926)	Atlantic Ocean and off Sumatra	Asano Filho <i>et al.</i> (2005); Costa <i>et al.</i> (2007); Pietsch (2009); Klautau <i>et al.</i> (2020); Melo <i>et al.</i> (2020)
Melanocetidae		
<i>Melanocetus johnsonii</i> Günther, 1864	Circumglobal	Pietsch, Van Duzer (1980); Pietsch (2009); Menezes <i>et al.</i> (2003); Melo <i>et al.</i> (2020); this study
<i>Melanocetus murrayi</i> Günther, 1887	Circumglobal	Pietsch, Van Duzer (1980); Menezes <i>et al.</i> (2003); Melo <i>et al.</i> (2020)
Thaumatchthyidae		
<i>Thaumatchthys binghami</i> Parr, 1927	Atlantic	Pietsch (2009); Melo <i>et al.</i> (2020)
Oneirodidae		
<i>Chaenophryne draco</i> Beebe, 1932	Circumglobal	Pietsch (2009); Melo <i>et al.</i> (2020); this study
<i>Chaenophryne ramifera</i> Regan & Trewavas, 1932	Circumglobal	This study
<i>Dolopichthys</i> sp.*	Off northeastern Brazil	This study
<i>Microlophichthys microlophus</i> (Regan, 1925)	Circumglobal	Pietsch (2009); Melo <i>et al.</i> (2020)
<i>Oneirodes anisacanthus</i> Regan, 1925	Atlantic	This study
<i>Oneirodes carlsbergi</i> (Regan & Trewavas, 1932)	Circumglobal	This study
<i>Oneirodes notius</i> Pietsch, 1974	Circumglobal in Southern Hemisphere	Figueiredo <i>et al.</i> (2002); Menezes <i>et al.</i> (2003); Melo <i>et al.</i> (2020)
<i>Pentherichthys atratus</i> (Regan & Trewavas, 1932)	Circumglobal	Pietsch (2009); Melo <i>et al.</i> (2020)
Caulophrynidae		
<i>Caulophryne</i> sp.*	Off northeastern Brazil	This study
Gigantactinidae		
<i>Gigantactis longicirra</i> Waterman, 1939	Atlantic and Pacific	Pietsch (2009); Melo <i>et al.</i> (2020)
<i>Gigantactis vanhoeffeni</i> Brauer, 1902	Circumglobal	Costa <i>et al.</i> (2007); Pietsch (2009); Mincarone <i>et al.</i> (2017); Melo <i>et al.</i> (2020)
<i>Gigantactis watermani</i> Bertelsen, Pietsch & Lavenberg, 1981	Atlantic and Pacific	This study
<i>Rhynchactis</i> sp.	Off northeastern Brazil	This study
Linophrynidae		
<i>Linophryne arborifera</i> Regan, 1925	Atlantic	Bertelsen (1980)

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ETHICAL STATEMENT

The authors state that all methods were approved and conducted in accordance with guidelines and regulations of the Brazilian Ministry of Environment (SISBIO authorization number: 47270-5). Operations of the RV Antea were approved by the Brazilian Navy Authority ("Estado-Maior da Armada") under the Ordinances 178 (08/09/2015) and 4 (24/01/2017).

COMPETING INTERESTS

The authors declare no competing interests.

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