

**Integrative taxonomy of *Anoplogaster cornuta* (Trachichthyiformes, Anoplogastridae)
from western North Atlantic: new insights**

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Abstract

Nineteen specimens of *Anoplogaster cornuta* (Trachichthyiformes, Anoplogastridae) were captured on Flemish Cap, western North Atlantic, by scientific surveys. Identification was carried out by integrative taxonomy, combining examination of morphological and molecular characters (DNA barcoding). Morphological examination confirmed several hitherto questionable taxonomic characters of the species, such as the presence of 8-9 branchiostegal

rays and 3-5 fang-like teeth on the lower jaw. As a result of the molecular analysis, 19 new sequences of cytochrome c oxidase subunit 1 *COI* were added to molecular repositories. DNA barcoding supports the morphological identification of the specimens of *A. cornuta* from the western North Atlantic and it also confirms the wide distribution range of the species. The combination of classical and molecular taxonomy has been useful for the delimitation and characterisation of this deep-water species, contributing to a better understanding of its intraspecific morphological and molecular variability.

Keywords: *COI*, taxonomy, barcoding, distribution, mitochondrial DNA, species identification

1. Introduction

The family Anoplogastridae is a small group of darkly-pigmented bathypelagic to mesopelagic fishes, with a body short, deep, and compressed, tapering to narrow peduncle. The head is large, with small eyes and a large mouth with huge fang-like teeth. Juveniles are very different, with pale bodies, large head spines, and no large teeth. The family contains only two very similar species in a single genus, *Anoplogaster cornuta* (Valenciennes, 1833) and *Anoplogaster brachycera* Kotlyar, 1986, with a circumglobal distribution in tropical and cold-temperate waters. The family Anoplogastridae, traditionally placed in the order Beryciformes, is now included in the order Trachichthyiformes (Moore, 1993).

Feeding mode is carnivore, preying on planktonic crustaceans as juveniles and on fishes and cephalopods as adults, being plastic ingestion also found in one individual (McGoran et al., 2021). In turn, they are preyed upon by large pelagic fish, such as tunas, lancetfishes, marlins and sharks. Piscivorous feeding makes this species among the highest trophic positions of meso- and bathypelagic predatory fishes (Richards et al., 2019).

Molecular taxonomy has been successfully implemented with the traditional morphological analysis in the systematic study of fishes. Thus, a variety of molecular markers such as the combination of *16S*, *COI*, *ND5+*, *H3* and *28S* (Chakrabarty et al., 2011), complete mitochondrial DNA sequences (Miya et al. 2003), the mitochondrial cytochrome c oxidase subunit I *COI* (Ross-Robertson et al. 2017), RH1 and RH2 opsin genes (Lupše et al., 2021) has been employed for taxonomic or phylogenetic purposes in *A. cornuta*.

Although deep-sea fish have been studied for a long time, our knowledge of their taxonomy, biogeography, evolution, phylogeny, basic biological traits, physiology, condition of stocks, fisheries, management, and conservation remain patchy (Orlov, 2022). The aim of this research is to use morphological data and the *COI* molecular marker in specimens caught in the western North Atlantic for taxonomic purposes, and to discuss the results in accordance with the data available in the scientific literature.

2. Material and Methods

2.1. Sampling data and morphological analysis

A total of 19 specimens of *A. cornuta* were caught in 2017 (FC2017) and 2021 (FC2021) during the annual EU Flemish Cap scientific bottom trawl survey carried out on board the R/V Vizconde de Eza in NAFO Division 3M.

Specimens were preserved frozen on board. Once in the laboratory, were defrosted at room temperature, examined and photographed in detail, and deposited in the fish collection of the Museum Luis Iglesias de Ciencias Naturais of Santiago de Compostela Galicia, Spain, with the reference numbers from MHN USC 25202-1 to MHN USC 25202-19. Identification of the specimens to species level was done according to Kotlyar (1986). Morphological

measurements were recorded with a digital caliper to the nearest mm. Standard length (SL) and head length (HL) were used throughout.

2.2. Molecular analysis

DNA was extracted from muscle, using the E.Z.N.A. Tissue DNA Kit (Omega BIO-TEK) according to the manufacturer instructions, with a single 100 μ L elution step. The 5' end of *COI* gene was amplified using 2 μ L of template DNA, the universal primer cocktail for fish DNA barcoding C_FishF1t1-C_FishR1t1 (Ivanova et al., 2007), and the Phire Green Hot Start II PCR Master Mix (Thermo Scientific), in a final volume of 20 μ L. The PCR cycling profile consisted of 30 s at 98 °C, followed by 35 cycles at 98 °C for 5 s, 52 °C for 10 s and 72 °C for 15 s, 72 °C for 1 min and cooling to 12 °C. PCR products were purified by treatment with ExoSAP-IT, subjected to sequencing reactions using the BigDye v3.1 cycle sequencing kit, and sequenced in both directions using the M13F (-21) and M13R (-27) primers (Messing, 1983), with a SeqStudio Genetic Analyzer (Applied Biosystems).

DNA sequence data, specimen photographs and other metadata have been deposited in the Barcode of Life Database (BOLD Systems; www.boldsystems.org) as part of the project entitled “Fishes of the Western Atlantic Ocean” (code FIWA), as Process IDs FIWA001-22–FIWA019-22. The barcode sequences have also been deposited in GenBank under accession numbers OQ211478–OQ211496.

Sequence quality was verified with MEGA v11 (Tamura et al., 2021) and, for each individual, direct and reverse sequences were assembled into a consensus sequence. The *COI* data were used (a) to double-check the morphological identification of voucher specimens via DNA barcoding and (b) to assess possible genetic structure across individuals from different sampling sites. For this, a Median Joining Network (Bandelt et al., 1999) was made with PopART 1.7 (Leigh & Bryant, 2015), with $\epsilon = 0$.

3. Results

3.1. Taxonomic account

Anoplogaster cornuta (Valenciennes, 1833) Fig. 1A–B

Hoplostethus cornutus Valenciennes [A.] in Cuvier and Valenciennes 1833: 470, South Atlantic, 26°S, 50°W (stomach content). Holotype: MNHN 0000-7443. Maul (1954): 30–37 (description, key); Grinols (1966): 305-306, description; Childress and Meek (1973): feed; Woods and Sonoda (1973): 387-393, description; Shimizu (1978): description; Kotlyar (1986): 136–142, description; Kotlyar (2003): 2, distribution; Balanov and Kharin (2009): 694-695, description; Tatsuta et al. (2014): 49-50, description.

3.2. Material examined

Nineteen specimens caught in Flemish Cap, western north Atlantic: MHN USC 25202-1, 131 mm TL, 18th June 2017, 47.5649 °N, -46.2650 °W, 1,168 m depth; MHN USC 25202-2, 162 mm TL, 18th June 2017; 47.5649°N, -46.2650 °W, 1,168 m depth; MHN USC 25202-3, 173 mm TL, 17th July 2021; 48.5215 °N, -44.4592 °W, 1,237 m depth MHN USC 25202-4, 159 mm TL, 26th July 2021; 47.6272 °N, -46.3718 °W, 1,131 m depth; MHN USC 25202-5, 153 mm TL, 19th July 2021; 48.7497 °N, -44.7937 °W, 1,328 m depth; MHN USC 25202-6, 162 mm TL, 17th July 2021, 48.5785 °N, -44.4628 °W, 1,380 m depth; MHN USC 25202-7, 138 mm TL, 19th July 2021, 48.7497 °N, -44.7937 °W; 1,328 m depth; MHN USC 25202-8, 148 mm TL, 18th July 2021, 48.7277 °N, -45.0838 °W; 1,209 m depth; MHN USC 25202-9, 148 mm TL, 26th July 2021, 47.5745 °N, -46.1977 °W; 1,003 m depth; MHN USC 25202-10, 151 mm TL, 4th August 2021, 46.3827 °N, -45.9668 °W; 499 m depth; MHN USC 25202-11, 161 mm TL, 18th July 2021, 48.741 °N, -45.1987 °W; 1,205 m; MHN USC 25202-12, 169 mm TL, 18th July 2021, 48.6500 °N, -45.0023 °W; 1,063 m depth; MHN USC

25202-13, 180 mm TL, 21th July 2021, 48.2138 °N, -46.3120 °W; 1,120 m depth; MHN USC
25202-14, xxx mm TL, 19th July 2021, 48.8773 °N, -45.1715 °W; 1,218 m depth; MHN USC
25202-15, xxx mm TL, 8th August 2021, 46.8733 °N, -43.8728 °W; 595 m depth; MHN USC
25202-16, 124.5 mm TL, 25th July 2021, 47.7452 °N, -46.2218 °W; 1,078 m depth; MHN
USC 25202-17, 139.6 mm TL, 26th July 2021, 47.7838 °N, -46.1397 °W; 988 m depth; MHN
USC 25202-18, 173.1 mm TL, 5th August 2021, 46.2717 °N, -45.6210 °W; 835 m depth;
MHN USC 25202-19, 157.6 mm TL, 18th July 2021, 48.7277 °N, -45.0838 °W; 1,209 m
depth

3.2. Description

Body deep and compressed tapering to narrow peduncle (Fig. 1A), body depth about two times in the standard length, from 1.9 to 2.5 in SL; head large, head length about one-third of the SL, 2.5-3.1 in SL, its depth greater than length and with many irregular grooves and ridges (Fig. 1B); snout obtuse, short and roundish, 3.1-6.7 in HL; eye small, eye diameter 5.2-6.6 in HL; mouth large and oblique, upper jaw slightly prominent, extending beyond the posterior margin of eye, its length 1.1-1.3 in HL; dorsal fin long, 2.3-2.7 in SL, inserted slightly posterior to pectoral fin origin; lateral line an open groove, bridged by scales at intervals; anal-fin base short, 9.9-11.5 in SL; pectoral fin long 3.1-4.3 in SL, sited behind the hind margin of operculum; caudal peduncle relatively slender, 9.3-12.2 in SL; 3 recurved canines in each side of the upper jaw and 4, rarely 3 or 5, in the lower; the anteriormost premaxillary and dentary teeth were considerably larger and pointed than the more posteriorly located ones and the lower longer than the upper; smaller teeth in a single row in both jaws; no teeth on vomer and palatines; pharyngeal teeth presents; denticulated gill rakers, ranging from a single cusp to a multifid tooth; dorsal fin rays 18 or 19, rarely 17; anal fin rays 8 or 9; pectoral fin rays 15, rarely 13, 14 or 16; pelvic fin rays 7; branchiostegal rays 8, rarely 9;

colour uniformly black. The main morphometric and meristic characters are showed in Table 1.

3.3. *Habitat and Distribution*

Adults inhabit mesopelagic, bathypelagic and abyssopelagic areas, as well as continental slopes and seamounts, while juveniles are often caught in epipelagic horizons and even near the surface (Kotlyar, 1986). Worldwide distribution in tropical to temperate and subarctic seas, with adults between 75 and 5,000 m depth, juveniles at 45-3,100 m and larvae at 2 m and more (Kotlyar, 2003). In the North Atlantic, its range extends from Greenland (rare) and Iceland to the equatorial Waters (Porteiro et al., 2017). In the Western Atlantic, occurs from St. Georges Bank to Falkland Islands (McEachran and Fechhelm, 1998). In the western north Atlantic *A. cornuta* is distributed along the American coasts south of the Gulf of Maine (Kotlyar, 1986), but also to Greenland and the Irminger Sea (Kenchington et al., 2018).

3.4. *Genetic features*

Fig. 2 shows a haplotype network of 652 nucleotides of the mitochondrial *COI* marker, where the contribution of the Flemish Cap sequences virtually doubles the number of previously existing public *A. cornuta* sequences, from 20 to 39. Five of the Flemish Cap sequences form new haplotypes, while the others share them with specimens from most of the existing locations in both the northern and southern hemispheres.

4. Discussion and conclusions

Although taxonomic research, as the oldest biological discipline for identification and description of species, has been carried out for more than 250 years, we are far from reaching this goal (Coleman, 2015). “Taxonomic impediment”, the taxonomic knowledge gaps, the

insufficient numbers of trained taxonomists and a lack of taxonomic infrastructure are greatly affecting knowledge of fish biodiversity. However, it is important to obtain accurate estimates of deep-sea fish diversity to develop efficient management and conservation methods (Teramura et al., 2022). Traditional taxonomy is descriptive, but the diagnostic characters of many hitherto unrevised fishes come from early manuscripts, which often refer to the examination of only a few specimens, and these results have come down to the present day with minimal changes (Bañón et al., 2022a). Molecular taxonomy has emerged in recent years as a powerful tool in the search for solutions in the taxonomic field and, more specifically, in the lesser-known deep-sea fishes. Therefore, integrative taxonomic studies combining morphology and molecular tools should be progressively applied in fishes, especially to less known deep-sea fishes, either to support the current taxonomic status, or the presence of crypticism or synonymy indicating hidden biodiversity (Bañón et al. 2021, 2022b).

The family Anoplogastridae has been taxonomically revised by Kotlyar (1986, 2003). Regarding the morphological description, the main characters of the examined specimens agree with those previously reported by other authors, but some questioned characters were clarified. Teeth as described by Kierdorf et al. (2022), with the anteriormost fang-like teeth longer and pointed, and the further posteriorly teeth shorter and more rounded exhibited, sometimes knob-like tips and a single row of minute equal sized teeth in both jaws (Kotlyar, 1986). The number of fang-like teeth in each side is three in the upper jaw and four in the lower jaw (Kotlyar, 1986; Balanov and Kharin, 2009). However, Maul (1954) found three on the premaxillaries of all five specimens examined, but four on the lower jaw in the largest specimen and three in the others. Only three fangs were found in the upper jaw, as described above; however, although four fangs were most commonly found in the lower jaw, three and five were also rarely found, extending the range of fangs for the species.

Kotlyar (1986) reports 8 branchiostegal rays for *A. cornuta*, noting that Woods and Sonoda (1973) report 8-9, but expand this range to 7–9 for the family (Kotlyar, 2003). Although 8 rays are the most usual count, specimens with 9 rays also occur, confirming the 8-9 range for this character. Pelvic fin rays are 7 in all of the examined specimens, which agree with previous counts (Maul, 1954; Woods and Sonoda, 1973; Kotlyar, 1986), although Tatsuta et al. (2014) reported 6-7 pelvic fin rays in three specimens of the Pacific Ocean.

The haplotype network does not suggest separation between sampling sites, as sequences of specimens from geographically distant sites such as the western Atlantic Ocean and Australia and New Zealand share haplotypes, suggesting the cosmopolitan nature of this deep-sea species. The addition of the new *A. cornuta* barcodes to the public databases is significant, as it virtually doubles the number of sequences available, but probably insufficient to be able to infer with confidence the genetic variability of the species.

Many meso- and bathypelagic fishes that are characterized by a worldwide distribution have highly divided population structure or include several cryptic species (de Carlos et al., 2020; Teramura et al., 2022). Apparently, this was not the case for *A. cornuta*, as both morphology and molecular taxonomy show evidence of a single species worldwide distributed.

As for its congeneric species *A. brachycera*, it is distinguished by the number of dorsal fin rays and the lengths of the temporal and preopercular spines (Kotlyar, 1986). However, no specimens of *A. brachycera* larger than 60 mm SL have been collected (Kotlyar, 2003) and distinctive differences could be ontogenetic, related to growth (Tatsuta et al., 2014). Currently, there are no available sequences for *A. brachycera* in public repositories. An integrative taxonomic study including molecular data should be applied to specimens of this species to confirm or disconfirm its validity.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The sequences employed in the current study are available in the BOLD systems (<https://www.boldsystems.org/>, accessed on 1 December 2022) and GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>, accessed on 1 December 2022) repositories. All specimens used in this study for taxonomical purposes are deposited in the fish collection of the Museo de Historia Natural, Universidade de Santiago de Compostela (MHNUSC) in Santiago de Compostela, Spain (see methods). All other data are included in this article.

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Fig. 1. (A) *Anoplogaster cornuta* MHN USC 25202-12, 169 mm TL; (B) Detail of the head and mouth showing the tongue and numbered fangs on the lower jaw in three specimens.

Fig. 2. Haplotype network of *COI* sequences of *Anoplogaster cornuta* (n = 39). Median Joining Network ($\epsilon = 0$) created in PopART v1.7. Each circle represents a haplotype; the size of circles corresponds to the number of individuals with the haplotype. Colours indicate sampling sites. Bars indicate the number of mutations between two haplotypes. Small black circles indicate hypothetical haplotypes, predicted by the model.