

Article

The Value of Correct Identification of Coastal Marine Fishes of Economic Importance: The Case of the Senegalese Tongue Sole (Pleuronectiformes: Cynoglossidae) in the Eastern Central Atlantic (Africa)

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Abstract

The Senegalese tongue sole, *Cynoglossus senegalensis*, includes three junior synonyms: *C. goreensis*, *C. guineensis* and *C. simulator*. In addition, *C. browni*, originally described as a subspecies of *C. senegalensis*, is currently considered a valid species. Recent observations of *C. senegalensis* specimens showed two different mouth morphologies, with mouth angle (i) not exceeding the posterior border of the lower eye and with a narrow interorbital distance (IOD) or (ii) exceeding that level and with a wider IOD. The first group represents *C. senegalensis*. The second, although containing the *C. browni* holotype, is named *C. goreensis*, following name priority. A third group, with a mouth angle not exceeding the posterior border of the lower eye and with an intermediately wide IOD, was also revealed. This last group suggests that *C. simulator* requires revalidation. DNA barcoding results confirmed all three species. This highlights that current *Cynoglossus* fishery statistics are based on doubtful identifications, probably skewing IUCN assessments. A pictorial guide is proposed to ease identification and help conservation assessments of policies and sustainable management plans for these economically important marine fish species. Common names in English, French and Kikongo (DRC) are proposed to facilitate communication with concerned local communities and to better spread the preservation/conservation message.

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1. Introduction

Cynoglossidae is economically the most important family of flatfishes in the world [1]. Based on the most recent available FAO capture data (for 2023, in [2]) for the Democratic Republic of the Congo (DRC), the country captures about 253,000 tons of fish, including 8000 tons in the Eastern Central Atlantic (ECA) marine fishing area. According to these capture data, the family Cynoglossidae (with no species or genera distinguished) is, with 410 tons (4.8% of marine catches), the sixth most important marine fish family of economic interest ([2]; see Supporting Materials [SM] for further information: Text S1). In addition, Cynoglossidae are an important source of animal protein and other essential nutrients, such as carbohydrates, fats, vitamins, minerals, etc., for the human body [3–6]. Finally, their fisheries are highly commercial in Africa, and these flatfishes are commonly sold on piers and in local markets where they are marketed fresh, frozen (as filets under their French name “filet de sole”), dried or smoked [6–8]. Nevertheless, in the DRC, *Cynoglossus* species are mainly purchased as luxury food. As such, they are found in some supermarkets, hotels and restaurants further upstream along the Congo River in Boma, Matadi and even Kinshasa, respectively, at about 90, 190 and even 510 km from Muanda (~5°55'60" S–12°21'0" E), along the coastline where they were originally landed (P.N., pers. obs. 2019). Furthermore, the Senegalese tongue sole, *Cynoglossus senegalensis* (Kaup 1858), and the Nigerian tongue sole, *Cynoglossus browni* Chabanaud 1949, the latter originally described as a subspecies of the former, are in fact two valid species found along the ECA coastline [8] and have been exported from Nigeria to Korea. Indeed, they are both sold at the Busan Jagalchi Market [7,8], the largest and most renowned international fish market in Pusan, South Korea. Nevertheless, available data on fishery statistics are unfortunately based on mixed species catches referring to Cynoglossidae, Pleuronectidae, and Soleidae [9,10]. Thus, catch statistics for individual *Cynoglossus* species are lacking [7,8,10–14]. Moreover, when comparing recent catch data with those from more than 15 years ago, there is a significant decline in the total biomass of catches of the *Cynoglossus* catch-all species assemblage [8,12,13,15].

Cynoglossidae are benthic fish found in tropical and subtropical seas [15–17]. They are found mainly on muddy or sandy bottoms of the continental shelf. However, they also occur in estuaries and ascend the lower part of rivers [8,11,16,18,19]. They are flat-bodied lanceolate fish, i.e., lance-shaped or tongue-shaped, compressed laterally and gradually decreasing in width backwards, with both eyes situated on the left side of their head, dorsal and anal fins confluent with the caudal fin, pectoral fins absent or rudimentary, and, usually, only the left pelvic fin (with four fin rays) present and located on the median line [8].

The family contains two subfamilies, Cynoglossinae and Symphurinae, three genera, and a total of 168 valid species [20]. The Symphurinae subfamily mainly differs from Cynoglossinae by: (i) a hooked snout (vs. not hooked), (ii) the lack of lateral line(s) on both sides (vs. present at least on the ocular side), and (iii) the pelvic fins being free from the anal fin (vs. confluent) [16]. Although containing only a single genus, *Symphurus*, the Symphurinae is the most speciose, with a total of 86 valid species known to date [20]. In contrast, the Cynoglossinae contains two genera, *Cynoglossus* and *Paraplagusia*, with a total of 75 and six valid species, respectively [8,16,20,21].

The species of the genus *Cynoglossus* are characterised by the presence of two or three lateral lines on the ocular side, that is, a mid-lateral and a margino-dorsal lateral line and sometimes also a margino-ventral one; a hooked snout combined with unfringed lips; and an inferior mouth [8,16,19,22–24]. In sub-Saharan Africa, the genus is known to occur along the coastlines of the following three FAO Major Fishing Areas [25–27]: (i) Area 34—the ECA, i.e., along the West African coast from Mauritania south to the mouth of the Congo River (DRC and Angola); (ii) Area 47—the Southeast Atlantic (SEA), i.e., along the East African coast from Angola to 30°00' E longitude in South Africa; and (iii) Area 51—the Western Indian Ocean (WIO), i.e., along the East African coast from a longitude of 30°00' E in South Africa up to Somalia [8,16,18]. To date, five valid *Cynoglossus* species are found in the ECA, with four being endemic to the region: *Cynoglossus cadenati* Chabanaud 1947, *Cynoglossus canariensis* Steindachner 1882, *Cynoglossus monodi* Chabanaud 1949, and *C. senegalensis*. All have been reported to occur along the entire coastline of the ECA from Mauritania to the Congo River mouth [25]. Instead, the fifth species, *C. browni*, has also been reported from the North Sea along the coast of the Netherlands, Northeast Atlantic (NEA) (FAO Major Fishing Area 27; [28]), North of Africa [29,30] and, although more doubtful, from both Angolan and South African coastlines, i.e., the SEA ([31]; Table A1 in Appendix A) (see Section 4).

Along the ECA coastline of Africa, some species of *Cynoglossus* even enter freshwater [32–34] and thus are also found in estuaries and freshwater lagoons [19,24,35,36]. Along the coastline of the Lower Guinea ichthyofaunal province (sensu [37]), it occurs in the freshwaters of the Ogowe River as far upstream as Lambaréné (Gabon), up to about 110 km from the coast, and in the Kouilou–Niari River (Republic of the Congo), up to about 160 km [19]. In the Congo Basin, *C. senegalensis* has also been found in freshwater (P.N., pers. obs. 2016), as far upstream as Loango–Nzambi (~6°53'6.5" S–12°48'29.6" E), which is about 75 km upstream from the Congo River mouth (L. Ngeli, Marine Mangrove Park [MMP] Ranger, pers. comm. 2022) [38]. It has been identified as a marine migrant, which usually reproduces in the sea, but whose juveniles and/or adults make significant use of the estuary environment as growth areas [39].

Cynoglossus senegalensis is currently classified as Near Threatened (NT) by the IUCN Red List [12]. The species is likely to decline significantly in many parts of its range, mostly if existing regulations to increase the mesh size of nets and to avoid the capture of juveniles are not further implemented, in areas such as Gambia and Nigeria [12]. Instead, *C. browni*, a former subspecies of *C. senegalensis* (see [40]) but now considered a full species [8,41], has been identified as Data Deficient (DD). Nevertheless, this species, along with other species of *Cynoglossus*, is targeted throughout its range by trawling [7,8,13].

During recent field expeditions (2013–2018 and 2018–2022) carried out in the MMP (DRC), covering its entire coastline and the right bank of the mouth of the Congo River (Arrêté Ministériel n° 0044/CM/ECN/92, 02.05.1992, creating and delimiting the MMP), *Cynoglossus* specimens were collected along the coastline and in the mangroves of the park, as well as upstream along the Congo River. In the field, these specimens were first preliminarily identified as *C. senegalensis* using the FAO species identification guide for fishery purposes of the ECA [8,42]. However, after closer observation, important differences in (i) the position of the posterior edge of the mouth compared to the posterior edge of the lower eye, (ii) eye size, and (iii) interorbital distance were noticed.

Therefore, to clarify this so-called intraspecific variation, a detailed integrative study, comprising qualitative (mouth phenotype) and quantitative (meristic, morphometric, and mitochondrial DNA [mtDNA] barcoding [COI]) data of specimens identified as *C. senegalensis* from our own field expeditions and some museum specimens, including all available type specimens, was undertaken. In addition, as *C. browni* was originally described as a subspecies of *C. senegalensis*, it is also included in this study. Furthermore, based on the

results obtained, an updated identification key to the *Cynoglossus* species of the ECA is provided. This key is also converted into a pictorial sheet, representing all six valid species of the region, to enable fast and accurate visual species identification in the field by fisheries agents. Finally, the case of *C. senegalensis* is here presented and discussed to illustrate and highlight (i) the crucial importance of sound taxonomic data; (ii) the necessity of voucher specimens for deposited DNA sequence data to enable future verification of past species identifications; (iii) the general lack of relevant taxonomic/biodiversity research on marine fish species of economic importance in the ECA; and (iv) its implication for much needed reliable fishery statistics and IUCN Red List assessments as primary information sources to guide more sustainable catches/landings and protect marine biodiversity.

2. Materials and Methods

2.1. Morphometrics

A total of 130 *Cynoglossus* specimens, including both syntypes of *C. senegalensis* and holotypes of *C. browni* and of *Cynoglossus simulator* Chabanaud 1949, a current junior synonym of *C. senegalensis*, were studied. In addition, for comparisons with *Cynoglossus goreensis* Steindachner 1882, only the original species description, photographs and X-ray of the holotype were used. Since it was not possible to loan the holotype, according to the Naturhistorisches Museum Wien (NMW) loan policy guidelines (A. Palandacic [NMW], pers. comm. 2017), they provided all data needed. Finally, the original description of the holotype of *Cynoglossus guineensis* ([43]: 104, figure 2) was used, as the holotype is considered lost (see below: historical overview). The two last (nominal) species are nowadays also considered junior synonyms of *C. senegalensis*.

Cynoglossus browni was included for two reasons: (i) the fact that it was originally described as a subspecies of *C. senegalensis* and (ii) the fact that re-examination of the holotype revealed that the species has a single lateral line on the blind side, as in *C. senegalensis*, confirming its overall similarity with the latter (see the overview of the taxonomic history section in the Results; Figure A1 in Appendix B).

Three meristics were taken on each specimen following Menon ([21]: figure 1a) and Munroe ([44]: figure 2d): (i) the number of scales on the mid-lateral line (LLS), (ii) the number of scales between the margino-dorsal and margino-ventral lateral lines (SBLL), and (iii) the total number of vertebrae (TNV). For the last count, X-rays were taken from radiographs using a VisiX-R-family device model DRR4 (by Medex Loncin S.A., Loncin, Belgium) for the RMCA specimens [45], a Faxitron 43855F (Tucson, AZ, USA) for the MNHN (type) specimens and a PARDUS portable X-ray (by ELTEKh Med, Ltd., St. Petersburg, Russia) for the NMW holotype.

One coded qualitative observation, the mouth code (MC), was added to the counts: the coding of the position of the fleshy mouth angle relative to the position of the lower eye (Figure 1; see [44]: figure 3). It was coded from 1 to 10, always based on the lower eye, as follows. **Codes 1 to 5:** a mouth angle that does not reach beyond the level of the posterior border of the lower eye, with **1** reaching, at most, up to the level of the anterior border of the eye; **2** reaching beyond the last level and, at most, up to the level of the first quarter of the horizontal eye diameter (HED); **3** reaching beyond the last level and, at most, up to the level of the middle of the HED; **4** reaching beyond the last level and, at most, up to the level of the first three quarters of the HED; and **5** reaching beyond the last level and, at most, up to the level of the posterior border of the eye. **Codes 6 to 10:** a mouth angle always reaching beyond the level of the posterior border of the lower eye, with **6** reaching beyond the last level and, at most, up to the level of the first quarter of the HED beyond the posterior edge; **7** reaching beyond the last level and, at most, up to the level of the middle of the HED beyond the posterior edge; **8** reaching beyond the last level and, at

most, up to the level of the first three quarters of the HED beyond the posterior edge; **9** reaching beyond the last level and, at most, up to the level of the posterior border of the HED beyond the posterior edge; and **10** always reaching beyond the level of the posterior border.

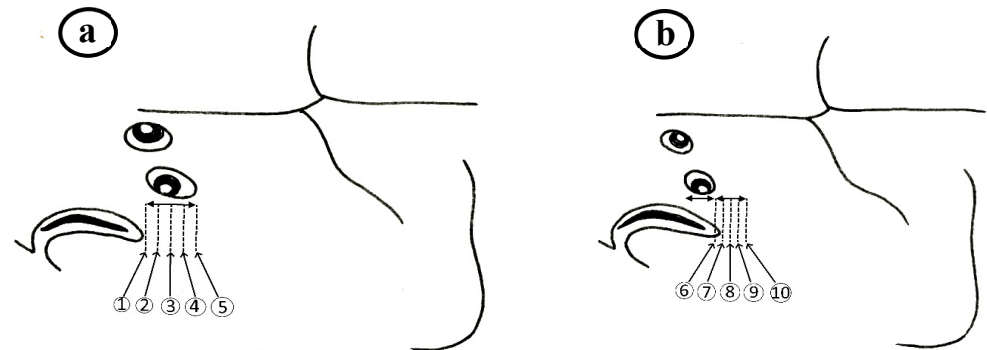


Figure 1. Schematic illustration of the relative position of the mouth angle vs. the posterior border of the lower eye. For further details about the coding, see the text. Note: 1 corresponds to the level of the anterior border of the lower eye. **(a) Codes 1 to 5:** the angle of the mouth not extending beyond the level of the posterior border of the lower eye (schematic illustration inspired by the head of a *C. senegalensis* specimen). **(b) Codes 6 to 10:** the angle of the mouth extending beyond the posterior border of the lower eye (schematic illustration inspired by the head of a *C. goreensis* specimen). Two different schemes are presented, as the eyes are larger in specimens with codes 1 to 5 compared to specimens with codes 6 to 10. This is important as the position of the mouth angle is described in relation to the horizontal eye diameter (HED), which is quite different between species in both groups (see Section 3. Results).

In addition, eight measurements were also taken on each specimen following Menon ([21]) and Munroe ([44]: figure 2A–C): (1) standard length (SL), (2) head length (HL), (3) body depth (BD), (4) head depth (HD), (5) horizontal eye diameter (HED), (6) snout length (sL), (7) vertical eye diameter (VED), and (8) interorbital distance (IOD).

Principal component analysis (PCA) reduces the number of variables to a few significant axes, i.e., the main components, which are a linear representation of the original variables. As such, PCAs were conducted to explore the meristic and morphometric multivariate data matrices [46]. Indeed, meristics and measurements were analysed separately, and specimens with missing values were case-wise deleted from the analyses [46,47]. For the meristics, a correlation matrix was used on the raw data, whereas for the measurements, a covariance matrix and the results expressed only as percentages were used because they proved to be more informative than the PCAs on the log-transformed data (see [48–51]).

Univariate non-parametric Mann–Whitney *U* tests (MWU-tests) with sequential Bonferroni correction [52] were performed for each character between species with more than four specimens studied for each (see [53]), in order to use only statistically representative samples. Nevertheless, these tests were not performed for samples/species measurements for which standard lengths were significantly different between samples/species ($p \leq 0.5$) [48]. Subsequently, the possible diagnostic value was visually scrutinised for all characters (counts and measurements) showing variation by plotting the raw counts against standard length (SL), in mm, and the percentage data of the measurements against SL, in mm, for measurements taken on the body, or against head length (HL), in mm, for measurements taken on the head. All statistical analyses were performed using STATISTICA version 8.0 for Windows [54].

A list of all the specimens examined is provided in the Supplementary Materials (see SM: List S1). Following the new policy of the RMCA, the collection numbers RMCA A0 up to A9 are listed as RMCA 2000–2009 and B0 up to B6 as RMCA 2010–2016. All locality data were translated into English.

2.2. Genetics

Genetic COI mtDNA analysis was performed on a total of 13 recently collected specimens. However, finclips or tissue samples were not available for historically collected and examined museum specimens. Although no voucher specimens were related to the COI sequences available on GenBank, they were nevertheless included in the genetic approach (see Section 4).

Obtaining high-quality COI barcode sequences for *Cynoglossus* samples was rather challenging. Various combinations of the primer set of Ward et al. ([55]) and Ivanova et al. ([56]) were tested. However, still with low sequencing success, the universal primer combination COI-3 for DNA barcoding with M13-tailed primers was the most effective [56]. The 25 µL PCR reactions included 2.5 µL PCR buffer (10×), 2.5 µL dNTP (2 mM), 1.25 µL primer cocktail (2 µM), 0.2 µL Taq DNA polymerase (5 units per µL; Taq Platinum, Invitrogen®), 2.0 µL of extracted DNA, and 16.75 µL of mQ-H₂O. The PCR profile was 3 min at 94 °C, followed by 35 cycles of 45 s at 94 °C, 40 s at 51 °C, and 1 min 30 s at 72 °C, ending with a final extension of 10 min at 72 °C [57]. Amplification was visually checked on 1.2% agarose gels and PCR products were purified using an ExoSAP-IT PCR Clean-up Kit (Thermo Fisher Scientific, Waltham, MA, USA). Standard Sanger Sequencing was executed by the external company MacroGen Europe, Amsterdam, the Netherlands, where samples were sequenced bidirectionally using an ABI 3730XL capillary sequencer. The DNA sequences were assembled and visually checked in CodonCode Aligner 4.2.7 (CodonCode Corporation, Centerville, MA, USA) and aligned and analysed in MEGA 7.02 [58].

Most of the 13 samples were successfully sequenced and contained ~650 bp of the COI gene, with the exception of two individuals: one with a very short sequence of 335 bp and the other with a shortened sequence of 528 bp. Additionally, a total of 49 GenBank sequences of *Cynoglossus* species occurring in the following FAO Major Fishing Areas were also added: ECA ($n = 5$ sequences), SEA ($n = 29$), NEA ($n = 1$), WIO ($n = 3$), Northwest Pacific (NWP) ($n = 3$) (FAO Major Fishing Area 61; [59]), and eight sequences from unknown localities (Table A1 in Appendix A). Complementary *Austroglossus pectoralis*, *Austroglossus microlepis*, and *Bothus podas* sequences from GenBank were included as outgroups following [31]. A model test was performed, and GTR + G + I was chosen as the most suitable model under the AIC criterion. Maximum Likelihood (ML) trees with 1000 bootstrap replications were produced.

Furthermore, average uncorrected p [60] and Kimura 2-parameter (K2P) [61] genetic distances (GDs) were calculated between and within the studied *Cynoglossus* species with MEGA [58]. These two distance metrics are routinely reported in DNA barcoding studies and enable direct comparison with other studies [62,63]. Both values are reported because p-distances do not account for multiple mutation hits in strongly divergent sequences, whereas K2P-distances tend to exaggerate species delimitation based on closely related sequences [60]. The newly obtained sequences ($n = 13$) of the newly collected and examined specimens were deposited in GenBank (GenBank accession numbers are listed in Table A1 in Appendix A).

2.3. Review of the Literature on the Most Important Fishes of Economic Importance for the ECA Since 2000

The proportion of taxonomic publications out of the total number of publications regarding the most economically important fish species of the most important fish families

in DRC fisheries (see FAO data above; introduction) was discussed. Within that framework, the literature on these species for the ECA as a whole was documented and reviewed using the following approach and criteria: (1) a publication was labelled as taxonomic if it contains at least a single (i) new species description or (ii) revalidation or synonymisation of a species, and (2) a publication was labelled as synthetic either if it presents a range extension of the distribution area of a certain species, which does not imply nomenclatorial changes, or new morphological and/or other evidence with regard to the delimitation of the species concerned.

To determine the taxonomic or synthetic nature of a publication, a Boolean search was conducted on Google Scholar per species, using its common names in English and French and its scientific name, together with “barcoding”, “revision”, “valid species” and “occurrence” as keywords, during an open time period.

2.4. Abbreviations

Abbreviations for museums and collections: AMNH: American Museum of Natural History, New York, USA; BMNH: British Museum of Natural History (for the fish collection of the NHM); IRSNB: Institut Royal des Sciences Naturelles de Belgique (for the collection of the RBINS); MNHN: Muséum National d’Histoire Naturelle, Paris, France; NHM: Natural History Museum, London, UK (for the institute); NMW: Naturhistorisches Museum Wien, Vienna, Austria; RBINS: Royal Belgian Institute of Natural Sciences, Brussels, Belgium (for the institute); RMCA: Royal Museum for Central Africa, Tervuren, Belgium; and RMNH: Rijksmuseum van Natuurlijke Historie (old name), now Naturalis-Nationaal Natuurhistorisch Museum, Leiden, the Netherlands.

Other abbreviations: COI: Cytochrome c Oxydase Subunit 1; DGD: Direction Générale de la Coopération au Développement, Belgium; DRC: Democratic Republic of the Congo; ERAIFT: Ecole Régionale postuniversitaire d’Aménagement et de gestion Intégrés des Forêts et Territoires tropicaux; FC: Frangs congolais; ICCN: Institut Congolais pour la Conservation de la Nature, DRC; K2P: Kimura 2-parameter; MWU-test: Mann–Whitney *U* test; PCA: principal component analysis; PC: principal component; MMP: Mangrove Marine Park, DRC; UAC: University of Abomey Calavy, Republic of Benin; UMN: Université Marien Ngouabi, Republic of the Congo; UNIBU: Université du Burundi, Republic of Burundi; and UNILU: Université de Lubumbashi, DRC.

3. Results

3.1. Contextualising the Taxonomic Issues: An Overview of the Taxonomic History of the Senegalese Tongue Sole

Cynoglossus senegalensis was described by Johann Jakob Kaup in 1858, originally as *Areliia senegalensis*, based on several specimens from West Africa. The author characterised the species by: (i) an interorbital distance equal to the diameter of the lower eye, (ii) two lateral lines on the ocular side (zenithal), and (iii) 126–130 dorsal, 109 anal and nine caudal fin rays [64]. To date, two syntypes (Figure 2a,b) are housed at the MNHN (B-2671 and IC-1999-0049), with the smallest (278.0 mm SL) collected in Gorée (Gorée Island: ~14°40' N–17°23' W) in Senegal [65], while the origin of the largest (520.0 mm SL) is unknown [41].

Later, in 1882, Franz Steindachner described *C. goreensis* based on a single specimen also from Gorée Island (Figure 3a) and collected by M.W. Höfler. Steindachner [66] differentiated *C. goreensis* from *C. senegalensis* by: (i) its lower number of scales along the lateral line, 104 (vs. 134–135 in *C. senegalensis*), and (ii) its larger size, up to 600 mm total length (TL) (vs. up to 555 mm TL).



Figure 2. Photographs of the ocular side (zenithal) of both syntypes of *Cynoglossus senegalensis*: (a) MNHN-B-2671 from Gorée Island (Senegal) (278.0 mm SL); (b) MNHN-IC-1999-0049 of unknown origin (520.0 mm SL) (© MNHN).

Subsequently, in 1909, Balthazar Osório [43] described *C. guineensis* also based on a single specimen (Figure 3b) from Bolama (~11°35' N-15°28' W) along the coast of Guinea-Bissau [67]. According to the author, this species differs from *C. senegalensis* by: (i) its lower number of scales between the two lateral lines, 16 (vs. 17–19 in *C. senegalensis*; see [32,35,68,69]), (ii) its shorter head length, being less than 16% of the total length (vs. more than 16% TL in *C. senegalensis*; see [11,32,68]), and (iii) its deeper body, more than 30% of head length (HL) (vs. 20–25% HL in *C. senegalensis*; see [32,68,70]). However, Osório [43] did not compare this species with *C. goreensis*. At present, the holotype of *C. guineensis* is considered lost due to a fire that ravaged and destroyed part of the Museu Bocage (see [71,72]).



Figure 3. Photographs of the ocular side (zenithal) of the holotypes of: (a) *Cynoglossus goreensis* (NMW 43776) from Gorée (Senegal) (550.0 mm SL) (© NMW); (b) *Cynoglossus guineensis* from the original description of the species by Osório (1909, figure 2) (330.0 mm SL) [40] (© MNHN).

Since 1909, tongue sole specimens identified as *C. senegalensis* have also been collected and reported from and around the mouth of the Congo Basin, i.e., Banana (~6°01' S–12°24' E), Malela (~5°59' S–12°37' E), Moanda (~5°56' S–12°20' E), and Vista (~5°52' S–12°17' E) in the DRC and Angola (collection databases: AMNH, 2022 and RMCA, 2022; see also [73]). Specimens from these localities are housed at the AMNH, RBINS and/or RMCA.

In 1949, Paul Chabanaud [40] reported that *C. senegalensis* is, in fact, a composite species. The author subdivided it into three morphs, now considered subspecies following the ICZN ([74], Article 45.6.4): *C. senegalensis senegalensis*, the nominal subspecies, and two new subspecies, which he named *C. senegalensis browni* (Figure 4a) and *C. senegalensis simulator* (Figure 4b). However, the use of a subspecies might be rather confusing in this case. Despite the definition of a subspecies as “an aggregate of local populations of a species inhabiting a geographical subdivision of the range of the species and differing taxonomically from other populations of the species” (see [75]: 430), regarding *C. senegalensis*, as far as is currently known, this does not seem to be the case. Nevertheless, according to Chabanaud [40], these subspecies can be distinguished as follows: *C. s. senegalensis*, with two zenithal (ocular side) and one nadiral (blind side) lateral line(s), 94–149 scales on the mid-lateral line, and 16–19 scales between the lateral line(s); *C. s. browni*, with two zenithal and 0 nadiral lateral lines, 98 scales on the mid-lateral line, and 17 scales between the lateral lines; and *C. s. simulator*, with three zenithal and one nadiral lateral line(s), 109 scales on the mid-lateral line, 17 scales between the synaxonal (middle) and epaxonal zenithal (upper) lateral lines, and a unique hypaxonal (lower) zenithal lateral line, which is incomplete and only 57 mm in length. The subspecies *C. s. browni* was described based on a single specimen, the holotype, collected by Jean Cadenat while on board the British trawler “Maid Honour” off the coast of Sierra Leone, named in honour of Dr. Brown, Director of the Fisheries Research Institute of British West Africa (MNHN 1949-023). According to Chabanaud [40], it is mainly characterised by: (i) the absence of the lateral line on the blind side (vs. presence in *C. s. senegalensis*) and (ii) the maxilla extending beyond the lower eye (vs. not extending beyond the lower eye in *C. s. senegalensis*). *Cynoglossus s. simulator* was also described based on a single specimen (holotype: MNHN-1949-022) purchased by Jean Cadenat at the market in Dakar (~14°41' N–17°26' W), Senegal [65]. According to Chabanaud [40], in *C. s. simulator*, the maxilla is situated under the lower eye (vs. not reaching the posterior border of the lower eye in *C. s. senegalensis* and extending behind the posterior border of the lower eye in *C. s. browni*). In addition, having been unable to highlight any discriminative criterion between the nominal species *C. goreensis* and *C. senegalensis*, although previously supposed to be different species, Chabanaud [40] synonymised both species, arguing that the number of dorsal and anal rays and the number of scales in the mid-lateral line vary considerably and thus cannot be used to distinguish between the two nominal species. Nevertheless, similar to Osório [43], Chabanaud did not compare *C. goreensis* with his composite species *C. senegalensis* [40].

Later, in 1959, Max Poll [11] published the scientific results of the fish of the Belgian Oceanographic Expedition in the African Coastal Waters of the South Atlantic (1948–1949). He also reported *C. senegalensis* from along the coast of the DRC and south of the mouth of the Congo River, off the coast of Angola [11]. Part of these collections was deposited in Belgium at RBINS, Brussels, and at RMCA, Tervuren. Unfortunately, the legend for the drawing of the *C. senegalensis* specimen in Poll (see [11]: figure 111bis) does not specify the origin or the size of the specimen (Figure 5a). Therefore, no rendering to an actual specimen housed in either of these Belgian institutions is possible. However, the mouth of this specimen reaches far beyond the posterior level of the lower eye, making it similar in this respect to the holotypes of both *C. goreensis* (Figure 3a) and *C. s. browni* (Figure 4a).



Figure 4. Photographs of the ocular side (zenithal) of the holotypes of both subspecies of *Cynoglossus senegalensis*, as described by Chabanaud [40]: (a) *C. s. browni* (MNHN 1949-023) from Dakar (Senegal) (222.0 mm SL); (b) *C. s. simulator* (MNHN 1949-022) from Sierra Leone (398.0 mm SL).

Subsequently, in 1977, Ambat Gopalan Kutty Menon [21], in his monograph of the genus *Cynoglossus*, elevated the subspecies *C. s. browni* to the species level and differentiated it from *C. senegalensis* by the absence of a lateral line on the blind side, as already noted in the original description of the subspecies by Chabanaud [40]. Furthermore, Menon [21] confirmed the junior synonymy of *C. goreensis* with *C. senegalensis*, as already introduced by Chabanaud [40], by considering the presence of a third lateral line in *C. goreensis* of no significance in terms of species distinction. However, no third lateral line was annotated for *C. goreensis* in the original description of the species by Steindachner [66] (see Figure 3a). In addition, Menon [21] identified *C. guineensis* as a new junior synonym of *C. senegalensis* by considering that (i) its slightly smaller scales and (ii) its deeper body, although reported to be diagnostic following Günther's data [76] on *C. senegalensis* (see [43]), only reflect intraspecific variation. Moreover, he also identified *C. s. simulator* as a new junior synonym since he did not consider an additional lateral line a significant difference for species distinction in *Cynoglossus*. Finally, Menon [21] identified 17 species complexes within *Cynoglossus*. One of them is the *C. canariensis* species complex, which he characterised by the (i) presence of 12 caudal fin rays and (ii) a single lateral line on the blind side, including five valid species, i.e., three from the ECA (*C. canariensis*, *C. monodi*, and *C. senegalensis*) and one from the WIO (*C. dubius*), both along the African coast, and one from the more distant East Indian Ocean (*C. borneensis*). *Cynoglossus browni* was indeed placed in a species complex on its own and, although still considered similar to the *C. canariensis* species complex based on its 12 caudal fin rays, it was, nevertheless, distinguished from it by: (i) the absence of a lateral line on the blind side (vs. one lateral line present in *C. canariensis*) and (ii) small eyes (vs. large eyes) separated by a wide interorbital space (vs. narrow interorbital space), small scales (vs. large scales), and a rounded snout (vs. pointed snout) (see [21]). Later, Menon [7] reported five known species of *Cynoglossus* in the ECA: *C. browni*, *C. cadenati*, *C. canariensis*, *C. monodi*, and *C. senegalensis*. Finally, in 2016, Munroe [8] also distinguished *C. browni* from *C. senegalensis* by the absence of a lateral line on the blind side (vs. presence of lateral line), the angle of the mouth reaching beyond the posterior border of the lower eye (vs. not reaching beyond the posterior border), and the presence of small eyes (vs. large eyes) (Figure 5b,c). In conclusion, to date,

only two valid species remain, *C. senegalensis* and *C. browni*, with *C. goreensis*, *C. guineensis* and *C. s. simulator*, all three being identified as junior synonyms of the first (see also [20]).

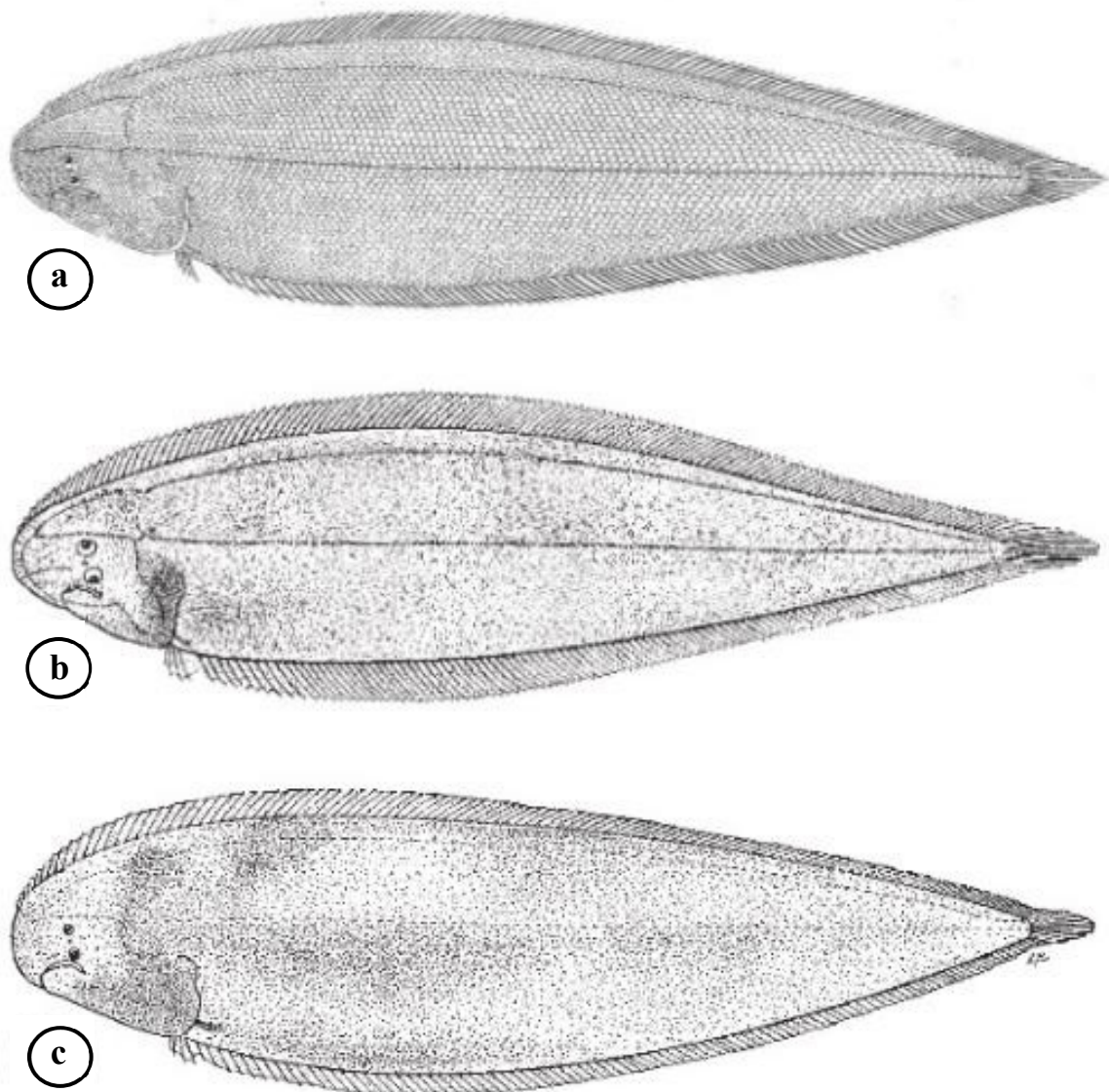


Figure 5. Drawings of the ocular side (zenithal) of some *Cynoglossus* of the *C. senegalensis* species complex: (a) *C. senegalensis*, as provided by Poll ([11]: figure 111bis), with the mouth reaching far beyond the posterior border of the lower eye; (b) *C. senegalensis* by Munroe ([8], © FAO); and (c) *C. browni* by Munroe ([8], © FAO). Unfortunately, no locality, size or voucher specimen data were provided by the authors.

3.2. Analyses of Counts and Mouth Codes

A first PCA was performed on three counts and one qualitative character, the mouth code (MC) of all examined specimens of the *C. senegalensis* species complex ($n = 130$). The highest loadings on PC1 are for the number of scales on the mid-lateral line (LLS), the MC, and the total number of vertebrae (TNV) (Table 1a). The highest loading on PC2 is for the number of scales between both lateral lines (SBLL).

A scatterplot of PC1 against PC2 for this PCA revealed, based on PCI loadings, the presence of three groups (Figure 6). The first group is located almost exclusively on the positive side of PC1 and includes the largest of both syntypes of *C. senegalensis*, here designated as its lectotype, and the barcoded specimens (i.e., specimens used in the genetic

analysis [see below]) identified as *C. senegalensis*. The second group is located entirely on the negative side of PC1 and includes both the holotypes of *C. goreensis* and *C. browni* and the barcoded specimens identified as *C. goreensis*. The third group, less obvious and between the previous groups, is located mostly on the negative side of PC1 and includes the holotype of *C. simulator*, the smallest of both syntypes of *C. senegalensis* (here designated as its paralectotype), and a single barcoded specimen identified as *C. simulator*. No separation is observed on PC2, except for a contribution to the separation between *C. senegalensis* and *C. simulator*.

Table 1. (a) PC loadings for a principal component analysis performed on three counts and one qualitative character, the mouth code (MC), for the 130 *Cynoglossus* specimens examined. The most important loadings are in bold; (b) MWU-tests performed on three counts and one qualitative character (MC) included in the PCA for the 130 *Cynoglossus* specimens examined. Bold and underlined values: highly significant difference, $p \leq 0.001$ after Bonferroni correction; bold values: significant difference, $p \leq 0.05$ after Bonferroni correction; regular values: no difference, $p > 0.05$ after Bonferroni correction. gor = *C. goreensis* ($n = 49$); sen = *C. senegalensis* ($n = 61$); and sim = *C. simulator* ($n = 20$).

Counts and MC	a. PC Loadings		b. MWU-Tests		
	PC 1	PC 2	sen vs. gor ($n: 61$ vs. 49)	gor vs. sim ($n: 49$ vs. 20)	sen vs. sim ($n: 61$ vs. 20)
LLS	0.960461	0.038721	<u>0.000099</u>	<u>0.000000</u>	<u>0.166759</u>
MDMVLS	0.237528	0.966550	<u>0.000000</u>	0.955786	0.836069
TNV	0.794854	−0.223794	<u>0.000000</u>	<u>0.000000</u>	0.061158
MC	−0.851770	0.104359	<u>0.000000</u>	<u>0.000000</u>	0.030108

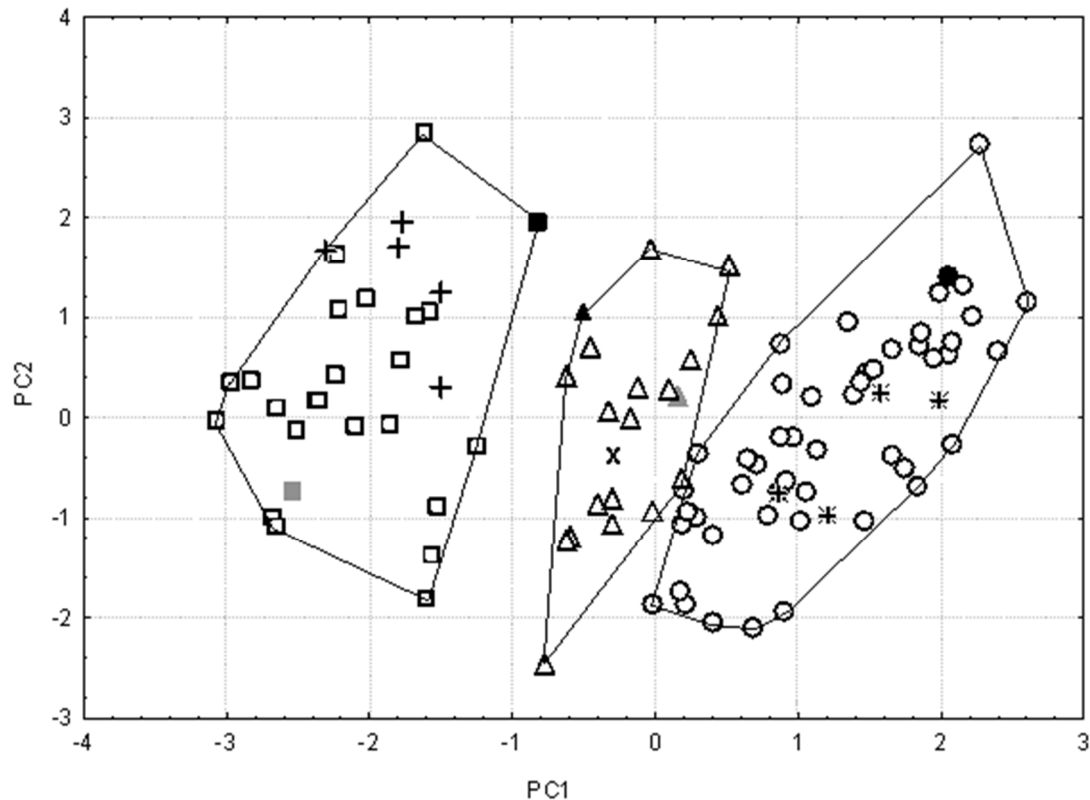


Figure 6. Scatterplot of PC1 against PC2 based on a principal component analysis of 3 counts and one qualitative character (mouth code: MC). *Cynoglossus goreensis*: ■, holotype; ■, holotype of *C.*

browni; □, other specimens; +, barcoded specimens. *C. senegalensis*: ●, lectotype; ○, other specimens; *, barcoded specimens. *C. simulator*: ▲, holotype; △, paralectotype of *C. senegalensis*; Δ, other specimens; X, barcoded specimen.

Mann–Whitney *U* tests with sequential Bonferroni correction were performed on all meristics and the qualitative character (MC) included in the PCA (Table 1b). All three meristics and the MC were found to be highly significantly different between *C. goreensis* and *C. senegalensis*. Furthermore, two meristics and the MC were found to be highly significantly different between *C. simulator* and *C. goreensis*. Finally, only the MC was found to be significantly different between *C. simulator* and *C. senegalensis*. Interestingly, besides the MC, both *C. senegalensis* and *C. simulator* were found to be highly significantly different from *C. goreensis* for at least two of the studied meristics (Table 1b).

Despite the fact that there are no major gaps between groups (i.e., [potential] species) and groups sometimes largely overlap, simple scatterplots confirmed the diagnostic potential of some of these meristics and the MC. First, the number of scales on the mid-lateral line (LLS) against SL (mm) shows mainly two groups, with *C. goreensis* having a lower number of mid-lateral line scales compared to both *C. senegalensis* and *C. simulator*, although with a small overlap with the latter (95 to 114 vs. 116 to 146 and 113 to 128, respectively) (Figure 7a).

Furthermore, a scatterplot of the MC against SL (mm) also revealed two groups. Indeed, the first one is composed of specimens with the posterior angle of the mouth situated after the posterior edge of the lower eye (MC = 6–10), here identified as *C. goreensis*. Instead, the second group is composed of specimens with the posterior angle of the mouth situated before or not exceeding the posterior edge of the lower eye (MC = 4–5 or only 5); here, they are identified as *C. senegalensis* and *C. simulator*, respectively (Figure 7b).

Finally, a scatterplot of the total number of vertebrae (TNV) against SL (mm) revealed two groups as well. Indeed, the first one, *C. senegalensis*, is composed of specimens with a high TNV, 59–63 (median: 61). Instead, the second group is composed of specimens identified as *C. goreensis* and *C. simulator* and contains specimens with a lower TNV, 57–59 (median: 58), for both these species (Figure 7c).

It should be noted that *C. goreensis* has higher MCs compared to both *C. senegalensis* and *C. simulator* (Figure 7b). Instead, *C. goreensis* has mostly a lower number of LLS, i.e., 95–114, compared to both other species, *C. senegalensis* and *C. simulator*, i.e., 106–146 and 108–124, respectively (Figure 7a). As such, *C. simulator* largely overlapped with *C. senegalensis* for both these characters (Figure 7a,b). As further illustrated in Figure 7a–c, this results largely from the fact that while *C. goreensis* and *C. simulator* both differ in their MCs (Figure 7b), *C. senegalensis* largely differs from *C. goreensis* in both the number of LLS and TNV, while *C. goreensis* mainly differs from *C. simulator* in the number of LLS only (Figure 7a,c).

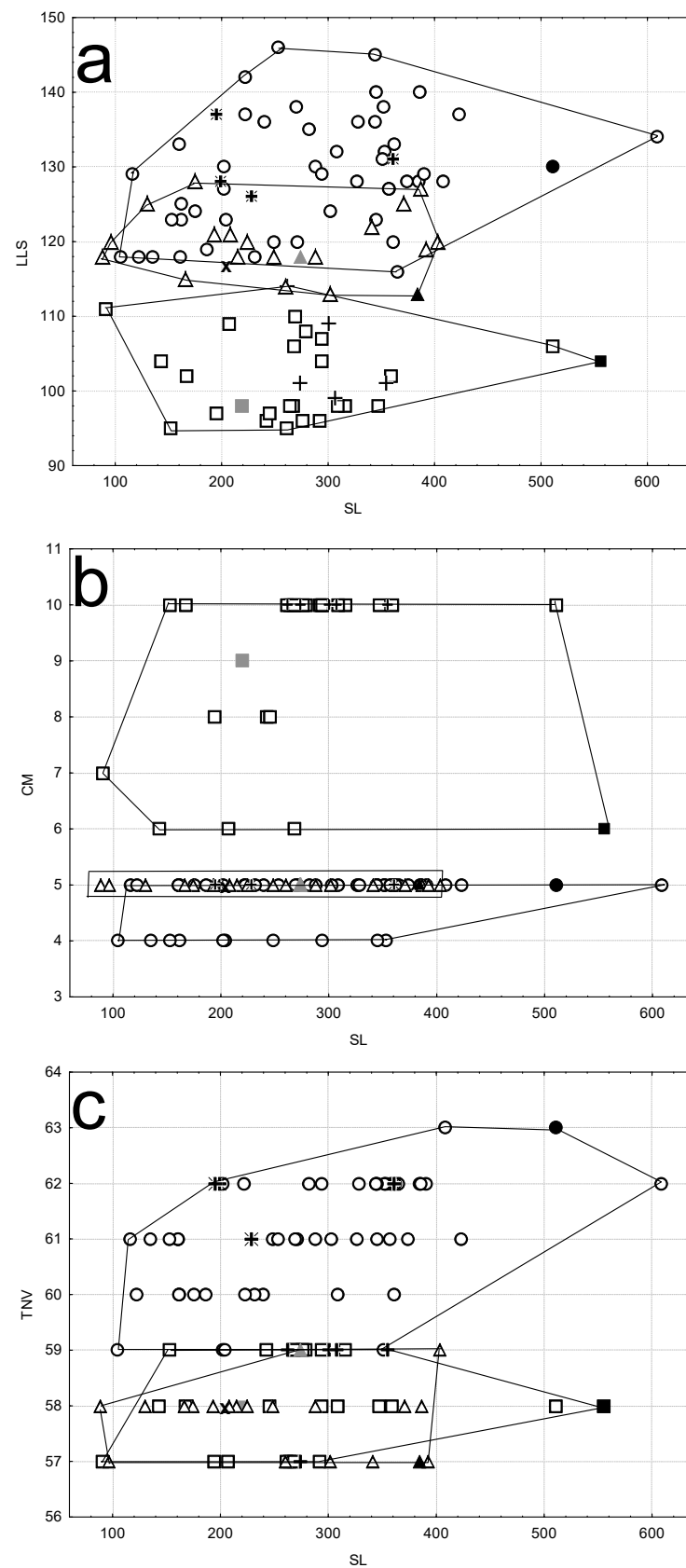


Figure 7. Scatterplots of: (a) the number of scales on the mid-lateral line (LLS) against standard length (SL; mm); (b) the mouth code (MC) against SL (mm); and (c) the total number of vertebrae (TNV) against SL (mm). *Cynoglossus goreensis*: ■, holotype; ■, holotype of *C. browni*; □, other specimens; +, barcoded specimens; ●, *C. guineensis*. *C. senegalensis*: ●, lectotype; ○, other specimens;

*, barcoded specimens. *C. simulator*: ▲, holotype; ▲, paralectotype of *C. senegalensis*; Δ, other specimens; X, barcoded specimen.

3.3. Analysis of Measurements

A second PCA was performed on seven measurements, expressed as percentages of SL or HL, for all specimens examined of the *Cynoglossus senegalensis* species complex ($n = 130$). The most important loadings on PC1 are for the body depth, the horizontal eye diameter, the interorbital distance, the vertical eye diameter and the head depth. On PC2, the most important factor loading is for the head length (Table 2a).

A scatterplot of PC1 against PC2 from this PCA revealed, based on PCI loadings, the presence of three groups (Figure 8), which turned out to be the same as the PCA on the meristics. The first group, located mostly on the negative side of PC1 and the positive side of PC2, includes the largest of both the syntypes of *Cynoglossus senegalensis*, here designated as its lectotype, the holotype of *C. guineensis*, and also the barcoded specimens (i.e., specimens used in the genetic analysis [see below]) identified as *C. senegalensis*. A second group, located mostly on the positive side of PC1 and the negative side of PC2, includes both the holotypes of *C. goreensis* and *C. browni* and the barcoded specimens identified as *C. goreensis*. The third group, located between the previous groups and mostly around the 0 point of PC1 (except for a single specimen), includes the holotype of *C. simulator*, the paralectotype of *C. senegalensis*, and a single barcoded specimen identified as *C. simulator*. This last group has a slight overlap with the second group, i.e., *C. goreensis*.

Table 2. (a) PC loadings of a principal component analysis performed on seven measurements in % for the 130 *Cynoglossus* specimens examined. The most important loadings are in bold. (b) MWU-tests performed on seven measurements included in the PCA for the 130 *Cynoglossus* specimens examined. Bold and underlined values: highly significant difference, $p \leq 0.001$ after Bonferroni correction; bold values: significant difference, $p \leq 0.05$ after Bonferroni correction; regular values: no difference, $p > 0.5$ for standard length and $p \geq 0.05$ for the remaining measurements after Bonferroni correction. gor = *C. goreensis* ($n = 43$); sen = *C. senegalensis* (51); sim = *C. simulator* (20).

Measurements	a. PC Loadings		b. MWU-Tests		
	PC 1	PC 2	sen vs. gor ($n: 51$ vs. 43)	gor vs. sim ($n: 43$ vs. 20)	sen vs. sim ($n: 51$ vs. 20)
Standard length (SL)			0.324862	0.176805	0.064673
Measurements in %					
Head length/SL	0.210194	−0.960530	0.000116	0.008356	0.743033
Body depth/SL	0.930563	0.037002	<u>0.000000</u>	0.008750	<u>0.000000</u>
Interorbital distance/HL	0.859159	−0.021322	<u>0.000000</u>	0.009160	0.000375
Horizontal eye diameter/HL	−0.886836	−0.088167	<u>0.000000</u>	0.004284	<u>0.000102</u>
Vertical eye diameter/HL	−0.857138	0.002672	<u>0.000007</u>	0.002214	0.119415
Snout length/HL	−0.612501	0.149871	<u>0.000000</u>	<u>0.000068</u>	0.008313
Head depth/HL	0.853317	0.236351	<u>0.000000</u>	<u>0.000028</u>	<u>0.000002</u>

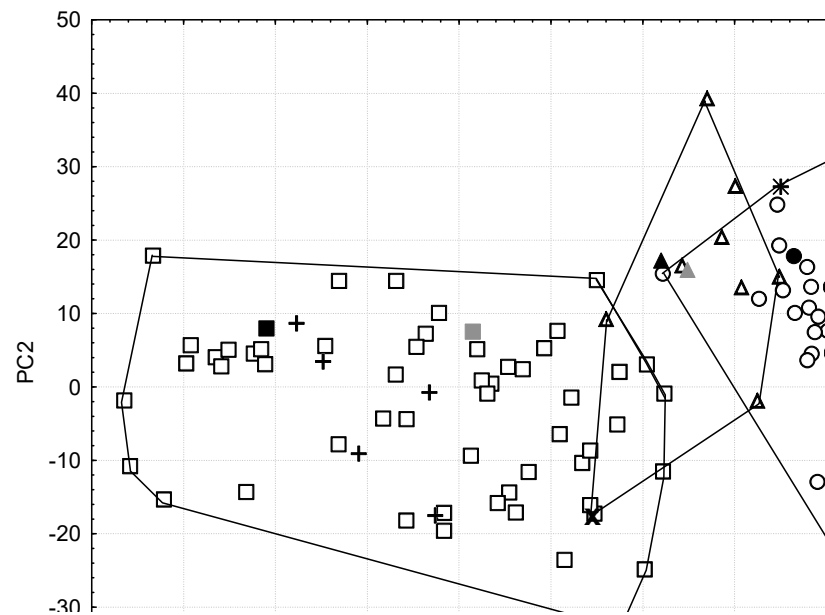


Figure 8. Scatterplot of PC1 against PC2 based on a principal component analysis of seven measurements (130 specimens), expressed in percentages. *Cynoglossus goreensis*: ■, holotype; ◼, holotype of *C. browni*; □, other specimens; +, barcoded specimens. *C. senegalensis*: ●, lectotype; ○, other specimens; *, barcoded specimens; ●, *C. guineensis*. *C. simulator*: ▲, holotype; ◄, paralectotype of *C. senegalensis*; Δ, other specimens; X, barcoded specimen.

Mann–Whitney U tests with sequential Bonferroni correction were performed on the seven measurements included in the PCA (Table 2b). For all comparisons, standard length (SL) was found to be not significantly different ($p > 0.5$). All measurements were found to be significantly different, with six highly significant, between *C. goreensis* and *C. senegalensis*. Furthermore, three measurements were found to be significantly different, with two of them highly significant, between *C. simulator* and *C. goreensis*. Finally, five measurements were found to be significantly different, with three of them highly significant, between *C. simulator* and *C. senegalensis*.

Again, despite the fact that (i) there are no major gaps between groups and (ii) groups sometimes largely overlap, simple scatterplots confirmed the diagnostic potential of at least some of these measurements. First, a scatterplot of the interorbital distance (IOD), as a percentage of head length (% HL), against standard length (mm) shows that *C. senegalensis* can largely be separated from *C. goreensis* (1.8 to 6.3 vs. 4.8 to 10.1% HL), with most of the overlap due to a single specimen only, identified as belonging to the latter species. Instead, *C. simulator* overlaps with both species (4.8 to 10.1% HL) (Figure 9a). Secondly, a scatterplot of body depth (BD), as a percentage of standard length (% SL), against standard length (mm) shows the presence of two large groups that partially overlap. The first one contains *C. senegalensis* specimens with a low body depth (17.4 to 22.8% SL). Instead, the second group contains *C. goreensis* and *C. simulator* specimens, usually with a higher body depth (21.9–27.2% and 21.9–24.1% SL, respectively) (Figure 9b).

3.4. Genetic Analyses

An ML tree based on the COI gene revealed that the 13 newly generated *Cynoglossus* sequences preliminarily attributed to the *C. senegalensis* species complex ($n = 9$) and to two more species, i.e., *C. canariensis* ($n = 3$) and *C. monodi* ($n = 1$), also identified among the recently collected specimens from the DRC and Benin ($n = 3$ and 1, respectively), cluster into five well-distinct clades (Figure 10). The results clearly show that *C. senegalensis* forms a distinct clade and is different from both *C. goreensis* (K2P genetic distance [GD]: 18.6%)

and *C. simulator* (GD: 16.4%). Furthermore, *C. goreensis* also forms a distinct clade from *C. simulator* (GD: 17.5%). Finally, *C. senegalensis* is also different from the two other *Cynoglossus* species identified between recently collected specimens from the DRC and Benin: *C. canariensis* (GD: 21.5%) and *C. monodi* (GD: 23.5%). Note that although both *C. canariensis* and *C. monodi* were revealed to be possible sister species (bootstrap support [BS]: 88), they still differ from each other by a large genetic distance (GD: 14.9%) (Table 3). Nevertheless, this GD is still a bit lower than the lowest interspecific GD found between the here-identified *Cynoglossus* species of the *C. senegalensis* species complex from the ECA, which is 16.4%, between *C. senegalensis* and *C. simulator* (see Table 3).

Furthermore, when comparing the newly generated sequences with those already available on GenBank, the following observations can be made with regard to the members of the *C. senegalensis* species complex as recognised herein: (i) The sequences of *C. senegalensis* ($n = 4$) from GenBank cluster together with a sequence here identified as *C. simulator* (GD: 3.6%) and do not clearly cluster together with our sequences of *C. senegalensis* (GD: 14.8%). Note that the GenBank *C. senegalensis* sequences were collected in Senegal and France, indicating a potential range extension and thus a larger distribution for *C. simulator*, which should, however, be further confirmed. (ii) The sequences of *C. browni* ($n = 3$) from GenBank cluster together with our sequences of *C. goreensis* (GD: 2.5%), which is in line with the proposed synonymy of the former with the latter. Finally, outside the *C. senegalensis* species complex, the following additional two observations can be made: (i) the sequences from GenBank identified as *C. canariensis* indeed seem to cluster together with the specimens here identified as *C. canariensis* (GD: 0.4%), and (ii) the single sequence from GenBank identified as *C. monodi* also clusters together with our unique sequence of *C. monodi* from the DRC, although still with a rather important genetic distance (GD: 6.9%).

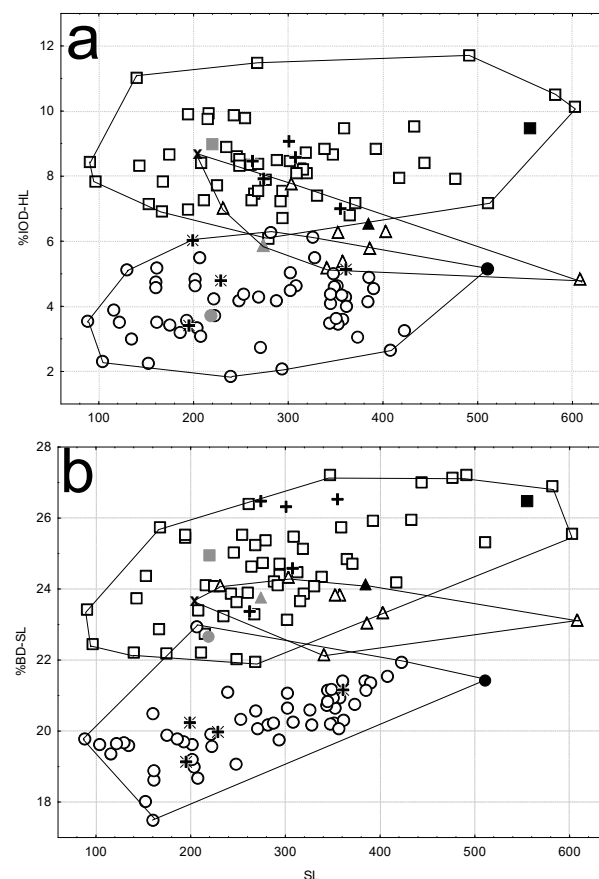


Figure 9. Scatterplot of: (a) the interorbital distance (IOD) (% HL) against standard length (SL) (mm); (b) body depth (BD) (% SL) against SL (mm). *Cynoglossus goreensis*: ■, holotype; ■, holotype of *C.*

browni; □, other specimens; +, barcoded specimens. *C. senegalensis*: ●, lectotype; ○, other specimens; *, barcoded specimens; ●, *C. guineensis*. *C. simulator*: ▲, holotype. ▲, paralectotype of *C. senegalensis*; Δ, other specimens; X, barcoded specimen.

Table 3. Average genetic distances (%) generated from the COI sequences between and within the *Cynoglossus* species, for newly generated sequences (own or not specified) and available GenBank (GB) sequences. K2P-distances and uncorrected p-distances between species separated by a diagonal, with the K2P-distances given above and the uncorrected p-distances (un. p) given below the diagonal. Dashes for species with only one specimen included.

Nr	Groups	Between Groups								Within Groups		
		1	2	3	4	5	6	7	8	9	K2P	un. p
1	<i>C. senegalensis</i> _own		18.6	23.5	21.5	16.4	14.8	22.2	18.8	20.5	0.002	0.002
2	<i>C. goreensis</i>	16.6		22.9	19.8	17.5	18.1	20.1	2.5	18.7	0.011	0.011
3	<i>C. monodi</i> _own	19.9	20.0		14.9	19.3	19.9	15.4	23.4	6.9	-	-
4	<i>C. canariensis</i> _own	18.7	17.8	13.6		20.4	19.9	0.4	19.9	13.7	0.003	0.003
5	<i>C. simulator</i>	14.5	15.8	16.9	17.8		3.6	21.3	18.3	14.7	-	-
6	<i>C. senegalensis</i> _GB	13.4	16.3	17.5	17.6	3.7		19.8	18.7	15.0	0.004	0.004
7	<i>C. canariensis</i> _GB	19.1	17.9	13.8	0.5	18.4	17.4		20.6	13.9	0	0
8	<i>C. browni</i> _GB	16.4	2.9	19.9	17.4	15.9	16.4	17.8		18.8	0	0
9	<i>C. monodi</i> _GB	17.8	16.8	6.6	12.5	13.2	13.6	12.5	16.5		-	-

3.5. An Integrative Synthesis

Based on the results of the morphological (counts, qualitative character and measurements) and mtDNA barcoding study, it follows that: (i) *C. goreensis* is to be revalidated with *C. browni* as its junior synonym, (ii) *C. simulator* is also to be revalidated and raised to the species level, and (iii) *C. guineensis* instead remains a junior synonym of *C. senegalensis*. In addition, both syntypes of *C. senegalensis* are not conspecific because the smallest, identified as a paralectotype, is conspecific with *C. simulator*. As such, this study reveals the existence of three valid species within what has for long been identified as a single species, *C. senegalensis*.

Furthermore, as a result, *C. senegalensis* is herein referred to as a morphological species complex whose members can be identified based on the occurrence of: (i) two complete lateral lines on the ocular side (vs. three in *C. canariensis*), (ii) 16–18 scales between upper and mid-lateral line (SBLL) (vs. 10–14 not only in *C. canariensis* but also in all other species of the ECA, *C. cadenati* and *C. monodi*, as part of the *C. canariensis* species complex, sensu Menon [21]), and (iii) an angle of the mouth not extending beyond the vertical from the posterior border of the lower eye, except for *C. goreensis* and a single specimen of *C. simulator* (vs. always extending beyond in *C. canariensis* and *C. monodi*). As such, *C. senegalensis* can thus be distinguished at least from *C. canariensis* itself and also from all species of the *C. canariensis* species complex, sensu stricto (s.s.), i.e., excluding *C. senegalensis*, contrary to the delimitation of the latter species complex by Menon [21] but still including *C. monodi*, which is also reported from the ECA [8,21], and both *C. dubius* (17–21 scales SBLL) and *C. borneensis* (18–20 scales SBLL) [21], which instead are known from the FAO Major Fishing areas 51 and 57, respectively [77,78].

In addition, within the *C. senegalensis* species complex, the three recognised species can morphologically be differentiated from each other as follows: (i) *C. senegalensis*, with its junior synonym *C. guineensis*, has a mouth angle not exceeding the level of the posterior border of the lower eye and a small interorbital distance (Figures 9a and 11a); (ii) *C. simulator*, including the paralectotype of *C. senegalensis*, has a mouth angle also not exceeding the level of the posterior border of the lower eye and an intermediary interorbital distance instead (Figures 9a and 11b); and (iii) *C. goreensis*, with its junior synonym *C. browni*, has

instead a mouth angle exceeding the level of the posterior border of the lower eye and a large interorbital distance (Figures 9a and 11c). An overview of the measurements and counts, per species as recognised in the present study, is provided in Table 4. Finally, the mtDNA barcoding results (Figure 10) for the sequenced specimens of the morphological *C. senegalensis* species complex revealed that they belong to three well-supported (BS = 100) and well-distinct clades (K2P GD ≥ 16.4 and an uncorrected p GD ≥ 14.5) (Table 3). As these three clades are congruent with the obtained morphological evidence, the species status of each of them is thus further affirmed.

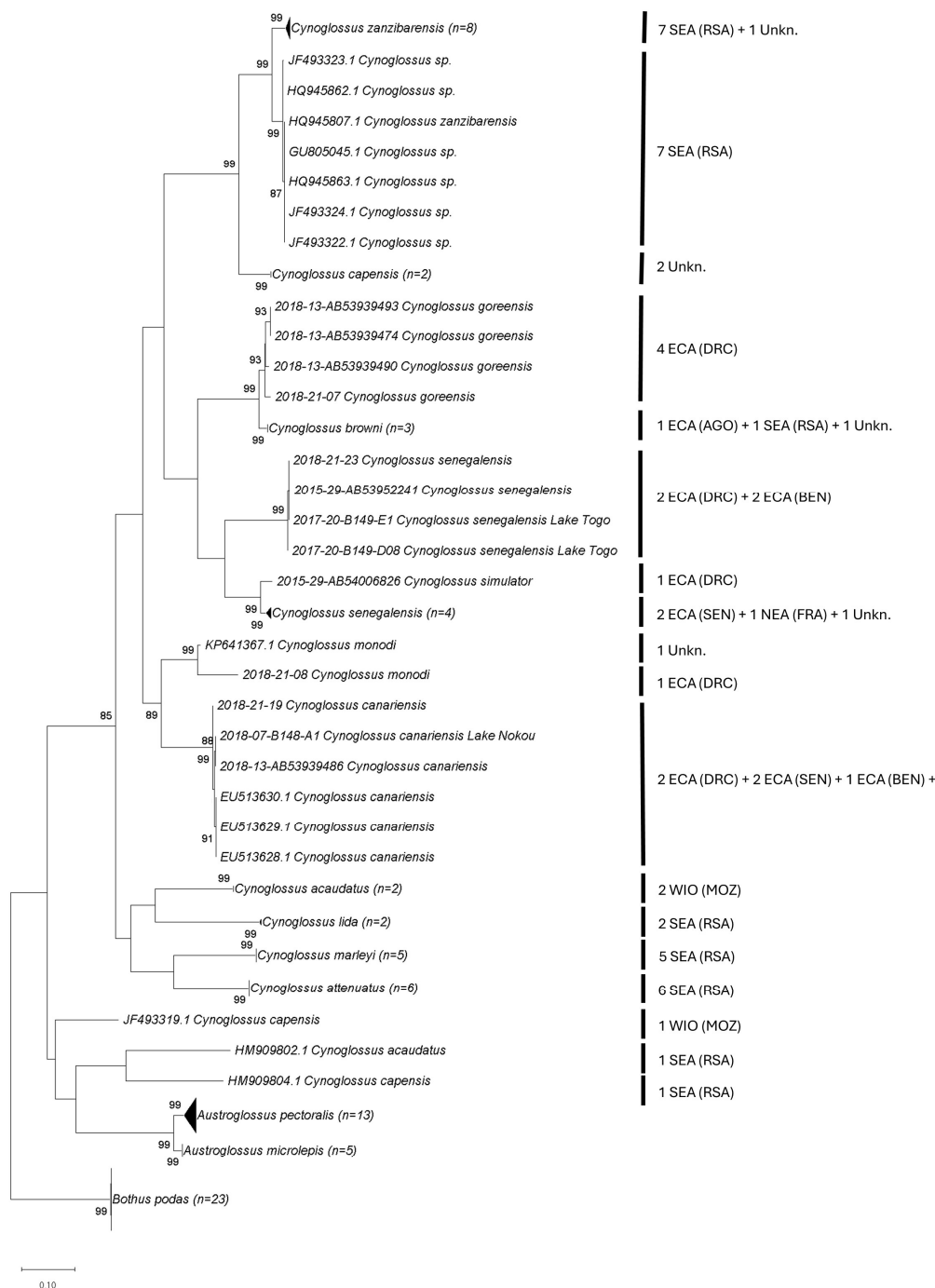


Figure 10. Rooted ML tree based on ~650 bp long *Cynoglossus* COI sequences. For the statistical node support (1000 bootstrap replications), only values >85 are indicated. Sequences retrieved from GenBank of the same morphospecies that form monophyletic clades are collapsed. Sequences generated

within the framework of the present study are indicated in grey. Country codes follow ISO 3166 alpha-3 [79]; SM: supermarket.

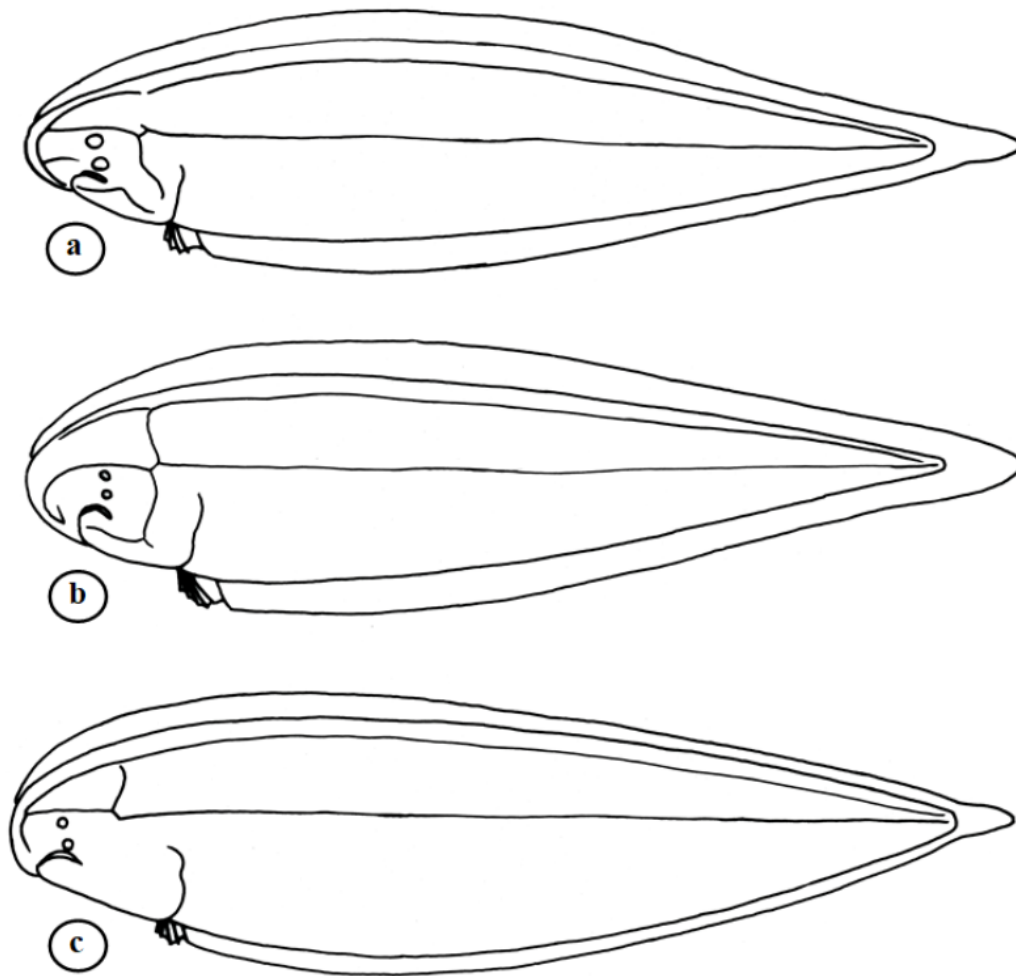


Figure 11. Schematic illustrations of: (a) *C. senegalensis*, (b) *C. simulator*, and (c) *C. goreensis* (drawings by Alain Reygel in 2018).

Table 4. Measurements and meristics of *Cynoglossus senegalensis*, *C. simulator* and *C. goreensis* (with SL = standard length, HL = head length, gui = *C. guineensis*, sen = *C. senegalensis*, bro = *C. browni*, ht = holotype, lt = lectotype, plt = paralectotype(s), and *n* = number of specimens included). Ranges include all representative specimens studied, i.e., the holotype (lectotype), and/or paratypes (paralectotypes). Dashes in cells with missing data. L = information from the literature; P = information from pictures.

Morphometrics	<i>C. senegalensis</i>					<i>C. simulator</i>					<i>C. goreensis</i>				
	lt	ht	gui ^L	min-max	mean	ht	plt	sen	min-max	mean	ht ^P	ht	bro	min-max	mean
	<i>n</i> = 58					<i>n</i> = 11					<i>n</i> = 60				
SL (mm)	511.1	218.5		88.3–511.1	267.8	384.4	274.2		203.9–608.7	340.3	555.5	219.3		91.0–602.7	295.9
Body measurements in %															
Head length (%SL)	83.6	35.0		18.7–83.6	54.8	66.5	47.7		37.3–105.5	60.1	99.5	39.6		18.9–109.4	55.8
Body depth (%HL)	109.5	49.5		17.5–109.5	46.9	92.8	65.1		48.3–140.6	79.9	147.1 ^P	54.7		21.3–156.6	73.8
Head measurements (%HL)															
Head width	85.3	36.4		16.0–85.3	44.4	76.9	53.2		43.2–119.6	62.9	120.5	45.5		21.8–129.5	61.5
Snout length	33.3	12.7		7.0–33.3	18.3	26.9	18.5		14.9–44.3	24.4	33.3	15.0		6.2–43.3	20.1
Horizontal eye diameter	8.7	4.8		2.2–9.2	5.5	5.7	4.6		4.1–10.0	5.7	8.7	2.8		1.7–8.1	4.2
Vertical eye diameter	8.5	4.0		1.9–8.5	4.6	5.7	3.9		3.7–10.0	5.4	5.8	3.0		1.5–7.0	3.6
Interorbital distance	4.3	1.3		0.5–4.3	1.9	4.3	2.7		2.7–5.0	3.8	9.4	3.5		1.6–11.5	4.7

Meristics	median					median					median	
Lateral line scales	130	-	108–146	124	108	118	108–134	120	104	98	95–128	109
Scales between dorsal and mid-lateral lines	17	10	10–19	17	18	18	15–18	17	17	16	16–21	17
Total number of vertebrae	63	-	57–63	61	57	59	57–62	59	58	58	57–59	58
Mouth code	5	4	4–5	5	5	5	5–6	5	7	9	6–10	8

3.6. An Updated Identification Key to the Species of the Genus *Cynoglossus* from the Eastern Central Atlantic (ECA)

The identification key presented is adapted from Munroe [8].

- 1a.** Three complete lateral lines on the ocular side (Figure 12a) *C. canariensis*
- 1b.** Two complete lateral lines on the ocular side **2**
- 2a.** Ctenoid scales on both sides of the body; 10 rays on the caudal fin; 11 or 12 scales between both lateral lines on the ocular side (SBLL); 68 to 72 scales in the mid-lateral line (LLS) (Figure 12b) *C. cadenati*
- 2b.** Ctenoid or cycloid scales on the blind side of the body; 12 rays on the caudal fin; 10 to 18 scales between both lateral lines on the ocular side (SBLL); 84 to 109 LLS scales **3**
- 3a.** Twelve to 14 scales between both lateral lines on the ocular side (SBLL); 85 to 96 scales on the mid-LL (LLS); and cycloid scales on both the ocular and the blind sides (Figure 12c) *C. monodi*
- 3b.** Seventeen to 18 scales between both lateral lines on the ocular side (SBLL); at least 108 LLS scales; and ctenoid scales on the ocular side and cycloid scales on the blind side **4**
- 4a.** Small eyes (4.2–8.8% HL); interorbital distance (IOD) wide (80.0–228.0% vertical eye diameter [VED]); mouth extending beyond (by at least a quarter of the eye diameter) the level of the posterior border of the lower eye (mouth code, MC: 6–10) (Figure 7b); and 108 to 128 (median: 109) LLS scales (Figures 3a, 4a and 11c) ..
..... *C. goreensis*
- 4b.** Large eyes (6.2–12.5% HL); IOD narrow, 18.9–76.4% VED; mouth not exceeding the level of the posterior border of the lower eye (MC: 1–5) (Figure 7b); and 108 to 146 (median: 124) LLS scales **5**
- 5a.** Mouth extending to the level of the posterior border of the lower eye (MC: 5) (Figure 7b); IOD at least always half the horizontal diameter of the lower eye (50.8–74.1, mean 62.4% VED) (Figures 2a, 4b and 11b) *C. simulator*
- 5b.** Mouth not exceeding the level of the anterior border of the last quarter of the horizontal diameter of the lower eye (MC: 1–4) (Figure 7b); IOD usually less than half the horizontal diameter of the lower eye (18.8–60.9, mean 39.8% VED) (Figures 2b, 3b and 11a) *C. senegalensis*

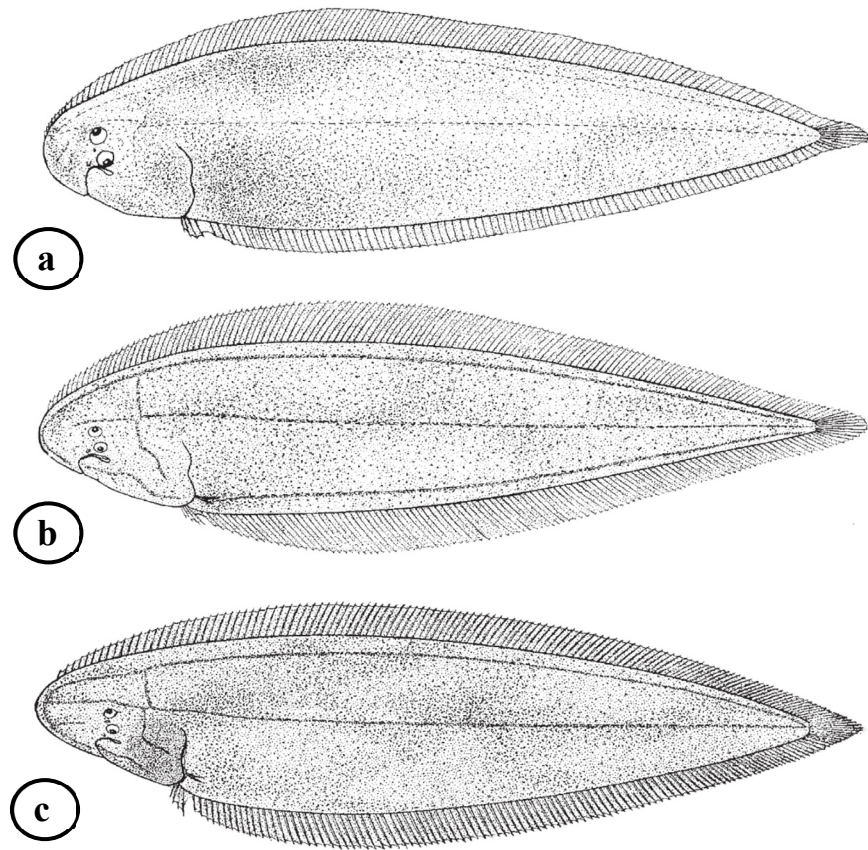


Figure 12. Illustrations of: (a) *C. canariensis*, (b) *C. cadenati*, and (c) *C. monodi*. All illustrations adapted from Munroe ([8], © FAO).

3.7. A Pictorial Identification Sheet for the Species of the Genus *Cynoglossus* from the Eastern Central Atlantic (ECA)

In addition to a traditional identification key, as used in fish taxonomy, a pictorial identification sheet is also presented for the ECA (Figure 13). This pictorial guide should enable easy identification of *Cynoglossus* species by any user without prior extensive and detailed taxonomic knowledge (e.g., some fisheries agents). Therefore, this pictorial identification sheet will help to provide more reliable species-based fishing statistics by addressing, through correct identifications, the recurrent problem of catch-all assemblages in *Cynoglossus* fishing reports. Indeed, multispecies or incorrectly identified species landings are one of the major problems in conducting reliable and meaningful stock assessments [80].

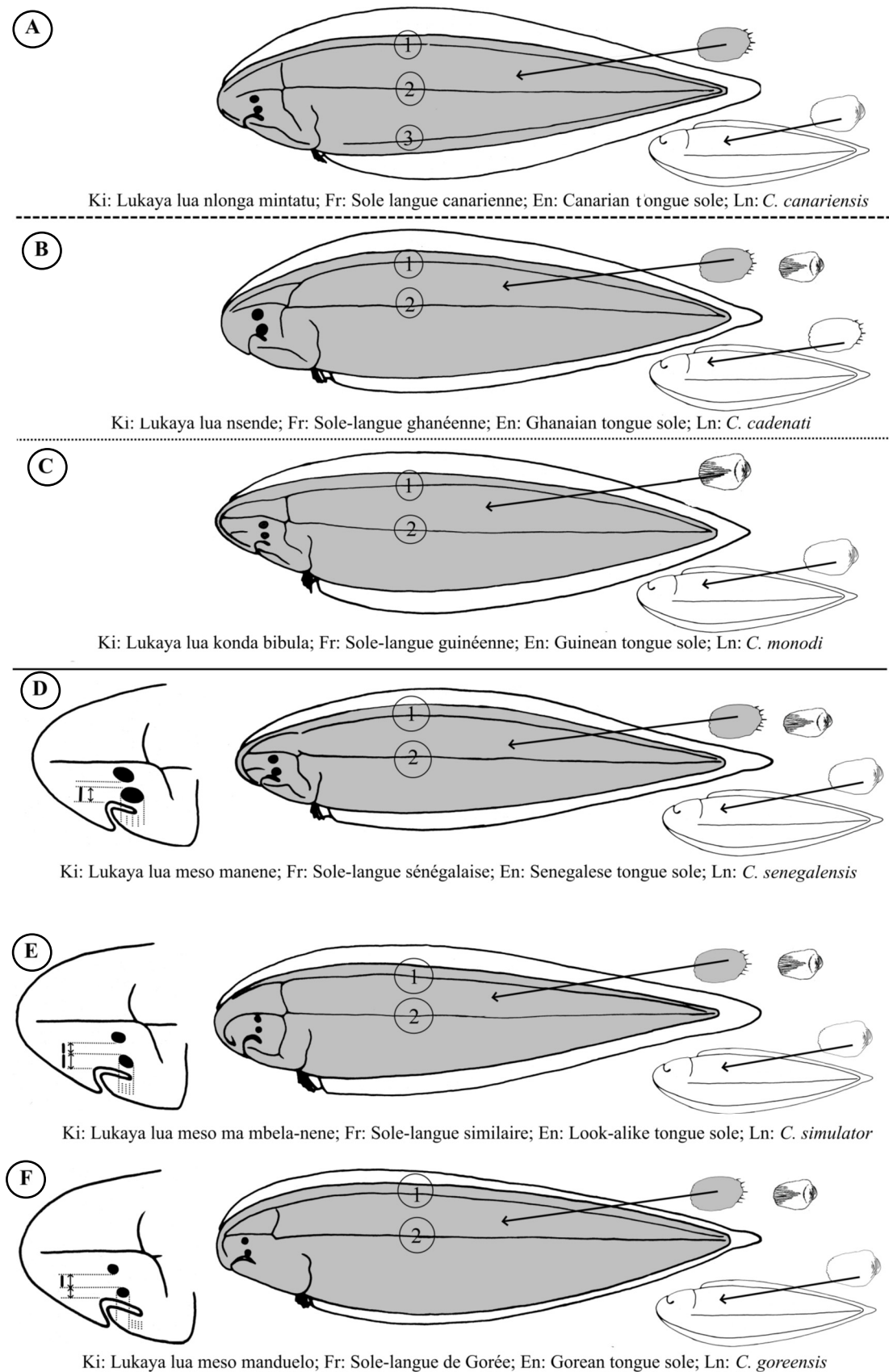


Figure 13. (A) pictorial identification sheet for the *Cynoglossus* species of the ECA. Ki: Kikongo of Boma (DRC), Fr: French, and En: English common names and Ln: Latin scientific name. Horizontal lines separate the first three species, one by one, according to the character states illustrated, while the last three species should be compared simultaneously. 1-2-3: Number of lateral lines present on

the ocular side; arrows indicate the type of scales present on the ocular side (in grey) and blind side (in white); in (D–F), head details showing the spacing between the eyes.

4. Discussion

4.1. Overview of the Different Taxonomic Decisions Taken: Which Is Which?

4.1.1. The Case of *Cynoglossus senegalensis*

In 1977, Menon [21] mentioned that the type specimen of *C. senegalensis* was not available in Berlin and is most probably not extant. Later, however, two syntypes of *C. senegalensis* were reported to be housed at the MNHN in Paris [41]. Nevertheless, these two syntypes are not conspecific. The largest specimen (MNHN 1999-0049: 520.0 mm SL), designated here as the lectotype of the species, corresponds to the original description of *C. senegalensis* by Kaup [64] according to its IOD, which is smaller than the vertical diameter of the lower eye (VED) (see Table A2 in Appendix A). The smallest specimen (MNHN B-2671: 278.0 mm SL), here designated as the paralectotype, has an IOD that is larger than the VED. Therefore, the paralectotype does not correspond to *C. senegalensis* but to *C. simulator* (see Figure 3a), thus indicating that its current taxonomic status should be re-examined soon. This is confirmed by an IOD more or less equal to the VED in *C. simulator* (vs. smaller in *C. senegalensis*). As no differences could be found between the holotype data of *C. guineensis* and *C. senegalensis*, the status of the former as a junior synonym of the latter is here confirmed.

4.1.2. The Revalidation of *Cynoglossus goreensis* and the Synonymisation of *Cynoglossus browni*

Cynoglossus goreensis, as described by Franz Steindachner ([66]: plate 1), differs from *C. senegalensis* by: (i) an IOD greater than the VED, with 80.0–228.0 (mean: 154)% VED (vs. smaller in *C. senegalensis*, 18.8–76.4 [mean: 47.6]% VED) (Figure 11a) and (ii) its mouth angle exceeding the posterior edge of the lower eye (vs. not exceeding). *Cynoglossus goreensis* is therefore a distinct species. Furthermore, based on Chabanaud's statement [40] in his original description of *C. browni*, all subsequent authors reported that *C. browni* indeed lacks a lateral line on the blind side [7,8,21,29]. Nevertheless, the reported absence of the lateral line on the blind side in *C. browni* is erroneous since its original description as a subspecies of *C. senegalensis* by Chabanaud [40] (see Figure A1 in Appendix B). As such, the holotype of *C. browni* (MNHN 1949-0023) and two additional specimens (MNHN 1967-0512 from Liberia and MNHN 1991-508 from Senegal) also match *C. goreensis*, as all three share the characters provided above to diagnose the species from *C. senegalensis*. Therefore, *C. browni* becomes a junior synonym of *C. goreensis* following the priority of names (ICZN 1999, Article 23.2, 23.3.5). The DNA barcoding results (Table 3, Figure 10) also support its species status, distinct from *C. senegalensis*.

4.1.3. The Revalidation of *Cynoglossus simulator*

Since its original description by Chabanaud [40], *C. s. simulator* has never been illustrated or used as a valid (sub)species (see [71]). However, according to our study, this nominal (sub)species is similar to *C. senegalensis* because its mouth angle does not extend beyond the posterior border of the lower eye (vs. extending in *C. goreensis*) and somewhat more similar to *C. goreensis* because it has a wider IOD compared to its VED, 80.0–228.0 (mean: 154)% VED (vs. inferior in *C. senegalensis*, 18.9–76.4 [mean: 47.6]% VED) (see Figure 11). As such, *C. simulator* was revealed to be clearly different from both *C. senegalensis* and *C. goreensis* and thus needs to be revalidated. The DNA barcoding results (Table 3, Figure 10) also support its species status, distinct from *C. senegalensis*.

4.2. *Cynoglossus senegalensis*: Illustrations of Pertaining Confusion

The fact that *C. senegalensis* has not been illustrated in its original description, as provided by Kaup [64], has certainly caused confusion about its identification. The various subsequent illustrations of the species found in the scientific literature surely reflect this long-standing problem. Indeed, while the current lectotype of *C. senegalensis* has a mouth angle that does not reach the posterior border of the lower eye, some old illustrations show that the mouth border extends well beyond this level. This indicates that what was previously identified as *C. senegalensis* is not a subspecies (see Tables A2 and A3 in Appendix A; Figure A2a,b in Appendix B; and SM: Text S2).

4.3. The Implications of the COI Barcoding Result on the Taxonomy of the *Cynoglossus senegalensis* Complex and the Importance of Voucher Specimens

About a decade and a half ago, Espiñeira et al. [31] undertook a study on the genetic identification of flatfishes with the special purpose of (i) correctly labelling the fishery products marketed, (ii) enhancing the traceability of raw products in the marketing chain, and (iii) fisheries control. Using two mitochondrial genes, Cytochrome b and COI, they included: (i) two specimens identified as *C. senegalensis* from Senegal and (ii) two specimens identified as *C. browni* from South Africa. For each of both species, however, three specimens were deposited in GenBank: (i) two from Senegal and one with no specified locality for *C. senegalensis* and (ii) one from Angola, one from South Africa, and one with no specified locality for *C. browni* (Table A1 in Appendix A). Unfortunately, no further details on localities or voucher specimens were provided by Espiñeira et al. [31].

Based on the current study's findings, *C. browni* was revealed to be a junior synonym of *C. goreensis*, but the former is not known from South Africa, as it is considered endemic to the ECA, i.e., from the coastline of Mauritania to Angola [8], except for a few specimens collected in the Northeast Atlantic (NEA), i.e., the Netherlands [29,30]. In addition, all three *C. senegalensis* COI sequences from Espiñeira et al. [31], as well as an additional one from a supermarket in France [81], are similar to our sequence of *C. simulator* (K2P GD between both = 3.6%, against GD = 14.8%, with the specimens identified as *C. senegalensis* by the current study). Interestingly, this illustrates that members of the morphological *C. senegalensis* species complex, such as *C. simulator*, are indeed indiscriminately exported to Europe (i.e., France, supermarket in department code 77) (see Figure 10, Table A1 in Appendix A). Finally, their three identified *C. browni* COI sequences are rather similar to our *C. goreensis* sequences (K2P GD between both = 2.4%, against GD = 18.7%, with specimens identified as *C. senegalensis* by the current study). However, due to the lack of voucher specimens, no morphological verification, and thus no reidentification, of these so-called reference sequences can be undertaken.

Hence, as illustrated above, voucher specimens are of crucial importance for verifying the original labelled voucher identification of fishery products [82–85]. Indeed, within this context, the greatest value of voucher specimens lies in the fact that they offer opportunities for future study and thus for future verification of past identifications [86–90].

4.4. The Need for Uniform and Species-Specific Vernacular Names

Different countries use different official vernacular names for the same species. Uniform and species-specific locally used vernacular names are important for communicating hidden species diversity to local (fisher) communities and highlighting the importance of protecting locally co-occurring biodiversity. Indeed, binomial scientific names are difficult to use when communicating with local (fisher) populations. In addition, correct and uniform vernacular names are also important at a local scale as they enable the gathering of correct fishery statistics. Moreover, tools such as the presented pictorial identification

sheet (see Figure 13) are needed to allow a quick, easy, reliable, and economic identification of fishery products at the original catch site and at markets. These tools are also used to check and verify the correct labelling of the product, both by commercial agents and local authorities [91]. As such, vernacular names in English, French, and a local language for each of the four valid *Cynoglossus* species and both of the newly revalidated species, *C. goreensis* and *C. simulator*, from the ECA are listed or proposed (Table 5). However, local names used are often more generic than specific, at least in some fish groups [92]. For instance, *Cynoglossus* spp. are all named “lunguadi”, meaning tongue and referring to their tongue-like shape (DRC), but also “lukaya” (in local Kikongo of Boma, the most widely spoken Bantu language in the MMP by the two majoritarian peoples, the Asso-longo and Woyo), meaning leaf, referring to their leaf-like shape. Here, the name “lukaya” is chosen for its traditional use in the DRC research area of the present study. However, it is extended with an appropriate name to be able to refer to each species separately and to better communicate the message of hidden species diversity locally (Table 5).

Table 5. Vernacular names (in Kikongo, French and English) for all six *Cynoglossus* species known to occur along the ECA coast. *Cynoglossus cadenati* is added, although it has not yet been reported from the DRC based on confirmed voucher specimens. D: Distinctive character used in the suggested Kikongo name. * Literal translation of the English names combining the distinctive character. References for existing English vernacular names only.

Scientific name	Kikongo of Boma	French	English	D. character	References
<i>Cynoglossus cadenati</i>	Lukaya lua nsende *	Sole-langue du Ghana	Ghanaian tongue sole	Ctenoid scales [9]: 3036	
<i>C. canariensis</i>	Lukaya lua nlonga ntatu *	Sole-langue Canarienne	Canary tongue sole	Three lateral lines [9]: 3037	
<i>C. monodi</i>	Lukaya lua konda nsende *	Sole-langue de Guinée	Guinean tongue sole	Cycloid scales [9]: 3038	
<i>C. goreensis</i>	Lukaya lua meso manduelo *	Sole-langue de Gorée	Gorean tongue sole	Small eyes [21]: 31	
<i>C. senegalensis</i>	Lukaya lua meso manene *	Sole-langue Sénégalaise	Senegalese tongue sole	Big eyes [9]: 3039	
<i>C. simulator</i>	Lukaya lua meso mambelane *	Sole-langue similaire	Look-alike tongue sole	Medium eyes	Current study

Note: Although *C. goreensis* has been referred to as *C. browni* in the past (see e.g., [8]), we did not want to use the English name, Nigerian tongue sole (see e.g., [8]), for the latter nominal species here. Instead, as its scientific name is now *C. goreensis*, we preferred to use the common English name for the latter, as used by Menon ([21]: 31). This was done to: (i) avoid confusion with regard to its old scientific name and thus, also, its vernacular appellation in English, and (ii) to provide as much uniformity in the common English names as possible. Indeed, except for one species, all others also have a geographically situated name.

4.5. The Importance of Correct Identifications and Their Implications for Fishery Data, IUCN Status Assessments and the Protection of the Marine Fish Species Considered

Cynoglossus senegalensis is the most common and abundant *Cynoglossus* species throughout its range, especially in estuaries, and is harvested with other *Cynoglossus* species in trawl fisheries [8,12]. Munroe [8] reports a significant decline in biomass in *Cynoglossus* catches compared to data from more than 15 years ago. On the other hand, according to FAO [2,10], world production of Pleuronectidae, Cynoglossidae, and Soleidae by capture fisheries was 962,545 tons in 2017 compared to 918,840 tons in 2002 [93], an increase of 4.8% over 15 years. Indeed, the DRC also reported a total of 120 tons of fished Cynoglossidae, for a total of 241,200 tons of fresh and marine fish in 2017, compared to 100 tons, for a total of 220,000 tons in 2002 [93], increasing 20% over 15 years. Despite their

relatively poor contribution to the DRC's overall yearly fish catch, *Cynoglossus* spp. are indeed of economic importance. In 2020–2022, they were sold at about 12,000 to 15,000 CDF (~6.5 to 8.0 USD) per kilogram, while other economically important marine fish, such as *Sardinella*, *Caranx*, *Galeoides*, *Pomadasys*, and *Pseudolithus* spp., are sold at approximately 6000 to 8000 CDF (~3.0 to 4.0 USD) per kilogram. Notwithstanding, *Cynoglossus* are “western-style” luxury food fish, i.e., they are bought by middle-high class people and consequently found in supermarkets and some high-standing hotels in the capital city, Kinshasa, well outside their natural range (P.N., pers. obs. 2022). Nevertheless, in many regions, particularly in Gabon, Guinea or Mauritania, the mixed catches of *Cynoglossus* spp. have declined by more than 60% in the past 5 to 25 years due to overexploitation [12].

Taxonomy and biodiversity issues are often neglected in fisheries management and trade-related issues [91]. For instance, flatfish species of different families (Pleuronectidae, Cynoglossidae and Bothidae) are all indiscriminately referred to as Soleidae due to the difficulty in identifying different species caught together by morphological characteristics [1,10,31]. *Cynoglossus browni* was assimilated to *C. senegalensis* in fisheries catch data following the global designation of soles. Furthermore, it was labelled Data Deficient (DD) in the IUCN Red List [13]. Although this might be partially due to its assimilation to *C. senegalensis* in fishing catches, it is also undoubtedly very rare in collections, which has been identified as one of the reasons for the species being classified as DD (see [80]: 1028). However, in addition, this classification most probably also results from its highly problematic identification due to (i) the previously reported absence of a lateral line on its blind side (see above), making the species unidentifiable, as the holotype has a lateral line on the blind side, similar to the other members of the *C. senegalensis* species complex, and (ii) *C. goreensis*, a former junior synonym of *C. senegalensis* [21], is here identified as a valid species and the senior synonym of *C. browni*.

Fishery catches attributed to *C. senegalensis* have led to the species being assessed as Near Threatened (NT) by the IUCN Red List [12]. However, based on the evidence presented in the current study, three different valid species have been lumped under this species assessment. As a result, these three valid species need to be reviewed in three distinct assessments. This situation will be challenging as it re-emphasises the need for correct taxonomic data, with the derived information essential for sustainable harvesting practices and protective measures that must be reliable and trustworthy.

In general, in the ECA countries, there are no formal measures to protect these fish, for instance, by (i) controlling the fishing gear used and (ii) increasing the mesh size of nets from 20 to 40 mm to avoid catching juveniles [1,12]. In Gambia and Nigeria, policies such as increasing the mesh size of nets have been put in place, but without serious monitoring and penalties for violations [12]. Therefore, *C. senegalensis* is likely to experience a significant decline in many parts of its range, which would likely lead to it being assessed as Vulnerable (VU) or Endangered (EN) today [12]. In addition to fishing, *C. senegalensis* is also affected by habitat degradation and pollution. However, juveniles are not considered to be targeted in most of their range, where adults are abundant [12]. Nevertheless, in some areas, juveniles are caught as by-catch during shrimp fishing and dried for local consumption [8]. Furthermore, most fishery statistics generally refer to groups of species and genera, rarely to species, and are generally based on vernacular names, which sometimes include many species [9,10,15]. This poses problems for the IUCN category assessments for these species. This is the case for the often-used appellation soles, which includes not only Cynoglossidae but also Pleuronectidae, Bothidae and Paralichthyidae.

The IUCN Red List assessment for species can be updated regularly, and a change in the category of a species on this list is an important indicator of the success or failure of conservation actions [80]. Regular evaluations of the IUCN category of fish species are necessary. However, this requires the correct identification of fish specimens caught [91].

To reliably report catches in the artisanal marine fisheries and to avoid mistaken identification by precisely identifying fish species and populations, as recommended by Fischer [91], it is important to develop and share some specific tools. These tools should enable the generation of reliable fishery data, which is critical to better monitor the management of these species. These data are urgently needed to develop sustainable fishery management and conservation plans for these economically important fish species. It is also essential to improve the monitoring, control, and surveillance of commercial fisheries [94]. Their sustainability is ensured by laws and regulations, but improving fisheries landing data requires the collection of real-time digital data, the standardisation of catch categorisation, and the integration of vessel tracking and trans-shipment control techniques. However, these methods still need to be refined to ensure the monitoring, control, and surveillance of all commercial fish species [94,95].

The importance of correctly identifying economically important marine fishes has been highlighted by the case of *Dipturus batis* (Linnaeus 1758), the large-sized “common skate” in the Eastern Atlantic (NEA, FAO area 27; [28]), assessed as the first case of a marine fish species endangered by overfishing [96]. Indeed, since the 1920s, two distinct species have been confused under the scientific name *D. batis* [97]. The largest species, the flapper skate (*Dipturus* cf. *intermedia*, 228.8 cm SL), largely disappeared thereafter due to overfishing, and a small-sized one, the blue skate (*Dipturus* cf. *flossada*, 143.2 cm SL), currently comprises the largest part of bottom-trawl catches [97]. The discovery of both skate species within one already listed as Critically Endangered (CR) illustrates similar problems to those highlighted in the *C. senegalensis* case.

The same kind of confusion holds true for an eagle ray of the Pacific Northwest (PN, FAO area 61; [59]). Indeed, *Aetobatus flagellum* (Bloch & Schneider 1801) has been fiercely hunted in Japanese waters as a pest species because of its so-called damage to commercial bivalve stocks. A taxonomic and mtDNA genetic study (COI and NADH2) led to the discovery of a new predatory species, *Aetobatus narutobiei* White, Furumitsu & Yamaguchi 2013. This species, rather than *A. flagellum*, is indeed predominant in these farmed bivalve stocks and is slaughtered annually as part of a predator control program. As a result, *A. flagellum* seems to have a more restricted distribution, with part of its former distribution covered by the new species [98]. Consequently, the IUCN status of *A. flagellum* as Endangered (EN) needs to be reassessed [98]. In both cases, as is partially true for *C. senegalensis* as well, a species other than the one currently under pressure has been targeted for fisheries and control programs, again illustrating the crucial need for and importance of reliable taxonomic information.

4.6. A General Lack of Biodiversity Research on Marine Fishes: The Case of the ECA

A review of the Cynoglossidae (*Cynoglossus*) literature for the ECA shows that, since 2000, there have been eleven major fish taxonomy/diversity publications on the five previously known *Cynoglossus* species in this FAO area. However, ten of them (90.9%) are of a synthetic nature (Tables A4–A6 in Appendix A), while only one publication (9.1%) [99] providing a new species description from the Red Sea can be identified as a taxonomic revision. As such, these publications fully reflect the status quo of the taxonomy/diversity level with not a single new synonym, new revalidation or new species for the ECA since 2000.

In general, our review of the literature for the six most important fish families (and subclass, i.e., Elasmobranchii) (see SM: Text S3) in the fisheries of the ECA shows that, since 2000, there have been 37 major fish taxonomy/diversity publications on the 47 economically most important species in this FAO area (Tables A4–A6 in Appendix A). About

three quarters (28 [75.7%]) are of a summarising nature and do not include a single taxonomic revision. Instead, less than one quarter (nine [24.0%]) are of some taxonomic nature at least (Table A4 in Appendix A).

Thus, the examples provided for the other fishes of economic importance (see SM: Text S3) in the marine waters of the ECA clearly illustrate that the existing situation is not unique to what has been referred to in the past as *C. senegalensis* and its congeners. Instead, it seems rather symptomatic of the situation found in other key species belonging to genera of fish families of major economic importance in the ECA. Therefore, it is hoped that with the present case study on *Cynoglossus*, renewed attention of all stakeholders in the field of fisheries and protection, i.e., preservation and conservation, will be drawn to the crucial need for reliable and correct biodiversity data on all economically important families, genera, and species of the ECA and even beyond.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/d18070440/s1>: List S1: Full list of examined *Cynoglossus* specimens; List S2: List of references for the economically important species of East Central Africa since 2000; Text S1: Five families preceding Cynoglossidae; Text S2: Illustrations of related confusion; Text S3: Most fished species by DRC fisheries. References [100–133] are cited in the Appendix. References [134–149] are cited in the Supplementary Materials.

Author Contributions: Conceptualisation, P.N. and E.J.W.M.N.V.; methodology, E.J.W.M.N.V.; formal analysis: morphology, P.N.; formal analysis: phylogenetics, E.D.; investigation, P.N.; fieldwork, P.N., S.W.L., and J.K.Z.; writing—original draft preparation, P.N. (lead) and E.J.W.M.N.V.; writing—review and editing, P.N. (equal), L.M.d.C. (equal), E.D., J.-C.M. (equal), and E.J.W.M.N.V. (equal); supervision, S.W.L. and J.-C.M. (lead); project administration, S.W.L. and E.J.W.M.N.V. (lead); funding acquisition, E.J.W.M.N.V. All authors have read and agreed to the published version of the manuscript.

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Institutional Review Board Statement: Not applicable.

Data Availability Statement: All mtDNA sequences are available in NCBI under their GenBank accession numbers (see Table A1 in Appendix A). Data are available upon request from the corresponding author.

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for the warm welcome and organisation of our study visit to the MNHN and the loan of some MNHN type specimens; and Esther Dondorp (Naturalis/RMNH) for the photographs of the specimens of *C. browni* (now *C. goreensis*) originating from the North sea along the Netherlands coast. Furthermore, we would also like to thank Djiman Lederoun (UAC) for collecting and thus making available some *Cynoglossus* specimens from Benin, which were also included in the present study. In addition, we would also like to thank Ngeli Pay (MMP), Dieudonné Kufulu and Pierre Manene, fishermen (MMP), for their regular participation in field expeditions (2014–2019). Finally, we would also like to express our gratitude to Wilungula Balongelwa, for their support of this work and to Marcel Collet (†2022), for his logistical support for the field trips (2013–2019) and for providing the permits needed to work in the MMP. The authors wish to express their gratitude to all three anonymous reviewers for their constructive comments to improve the manuscript. Finally, we would like to thank Paul H. Skelton for his time and valuable English-language editing.

Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

Table A1. Taxon names, voucher catalogue numbers and GenBank accession numbers for the newly generated and the GenBank-accessed COI sequences for *Cynoglossus*.

Taxon	Genbank	Tissue	Fishing Zone	Collection Locality
Museum Catalogue or Specimen	Access N°	Code	/Country	
<i>Cynoglossus acaudatus</i>				
voucher ADC08 Smith 261.1#2	JF493312.1	-	WIO/MOZ	Pomene
voucher ADC09_261.1#3	JF493311.1	-	WIO/MOZ	Pomene
voucher ADC09_261.11	HM909802.1	-	WIO/MOZ	Pomene
<i>Cynoglossus attenuatus</i>				
voucher Smith 261.2 #5	JF493318.1	-	SEA/RSA	Tugela Banks
voucher Smith 261.2 #7_05	JF493317.1	-	SEA/RSA	Tugela
voucher Smith 261.2 #6_05	JF493316.1	-	SEA/RSA	Tugela
voucher Smith 261.2 #2	JF493315.1	-	SEA/RSA	Tugela Banks
voucher Smith 261.2 #3	JF493314.1	-	SEA/RSA	Tugela/Banks
voucher Smith 261.2 #4	JF493313.1	-	SEA/RSA	Tugela/Banks
<i>Cynoglossus browni</i>				
Not specified	EU513625.1	isolate CbroI1	ECA/AGO	-
Not specified	EU513626.1	isolate CbroI2	SEA/RSA	-
Not specified	EU513627.1	isolate CbroII1	-	-
<i>Cynoglossus canariensis</i>				
Not specified	EU513628.1	isolate CcaI1	ECA/SEN	-
Not specified	EU513629.1	isolate CcaI2	ECA/SEN	-
Not specified	EU513630.1	isolate CcaII1	-	-
MRAC 2018-07-P-0001-0012	MK425171	2017-07 B148-A1	ECA/BEN	Lake Nokoue
MRAC 2018-013-P-0001-0005	MK425167	2018-013 AB53939486	ECA/DRC	Banana Littoral Km 4
MRAC 2018-021-P-0019	MK425162	2018-019 AB53939517	ECA/DRC	Banana Littoral Km 5
<i>Cynoglossus capensis</i>				
voucher ADC09_261.3#3	JF493319.1	-	SEA/RSA	Agulhas Bank
voucher ADC09_261.3#5.a	HM909804.1	-	SEA/RSA	Agulhas Bank
voucher_ADC09_261.35	GU804992.1	-	-	-
voucher_ADC09_261.31	GU804993.1	-	-	-
<i>Cynoglossus goreensis</i>				
MRAC 2018-013-P-0001-0005	MK425163	AB53939493 (short)	ECA/DRC	Banana Littoral Km 5
MRAC 2018-013-P-0001-0005	MK425164	AB53939474	ECA/DRC	Banana Littoral Km 5

MRAC 2018-013-P-0006-0007	MK425165	AB53939490	ECA/DRC	Banana Littoral Km 5
MRAC 2018-021-P-0007	MK425160	AB53939504	ECA/DRC	Banana Littoral Km 5
<i>Cynoglossus lida</i>				
voucher Smith 261.7 #2_05	JF493321.1	-	SEA/RSA	Tugela
voucher Smith 261.7 #1_05	JF493320.1	-	SEA/RSA	Tugela
<i>Cynoglossus marleyi</i>				
voucher ADC10_261.8 #2	HQ945839.1	-	SEA/RSA	Tugela Banks
voucher ADC09_261.8#1	HM421818.1	-	SEA/RSA	Tugela Banks
voucher ADC2013 261.8 #5	KU176455	-	SEA/RSA	Tugela Banks
voucher ADC2013 261.8 #4	KU176350.1	-	SEA/RSA	Tugela Banks
voucher ADC_261.8 #3	KF489562.1	-	SEA/RSA	Nhlabane Deep
<i>Cynoglossus monodi</i>				
Not specified	KP641367.1	isolate PKU 10423	-	-
MRAC 2018-021-P-0008	MK425161	2018-021 AB53939505	ECA/DRC	Banana Littoral Km 5
<i>Cynoglossus senegalensis</i>				
Not specified	EU513631.1	isolate CseI1	ECA/SEN	-
Not specified	EU513632.1	isolate CseI2	ECA/SEN	-
Not specified	EU513633.1	isolate CseII2	-	-
voucher FLID089	KP975542.1	-	NEA/FRA	Department code 77
MRAC 2017-020-P-0001-0002	MK425170	B149-D08	ECA/BEN	Lake Togo
MRAC 2018-021-P-0023	MK425159	AB53939497	ECA/DRC	Banana Littoral Km 5
MRAC 2015-029-P-0020	MK425166	AB53952241	ECA/DRC	Littoral Coastal Zone PMM
MRAC 2017-020-P-0001-0002	MK425169	B149-E1	ECA/BEN	Lake Togo
<i>Cynoglossus simulator</i>				
MRAC 2015-029-P-0022	MK425168	B5-029 AB54006826 (shortened)	ECA/DRC	Littoral
<i>Cynoglossus sp.</i>				
voucher ADC09_261.99#5	JF493323.1	-	SEA/RSA	Tugela Banks
voucher ADC10_261.99 #7	HQ945862.1	-	SEA/RSA	Tugela Deep
voucher ADC10_261.99 #8	JF493322.1	-	SEA/RSA	Tugela Deep
voucher ADC10_261.99 #4	HQ945863.1	-	SEA/RSA	Tugela Banks
voucher ACD07_261.99 #1	JF493324.1	-	SEA/RSA	-
voucher ACD09_261.99 #3	GU805045.1	-	SEA/RSA	Tugela Banks
<i>Cynoglossus zanzibarensis</i>				
voucher ADC10_261.9 #10	HQ 945807.1	-	SEA/RSA	Tugela Banks
Not specified	EU513637.1	isolate CzanII2	-	-
Not specified	EU513636.1	isolate CzanII2	-	-
Not specified	EU513635.1	isolate CzanI2	SEA/RSA	Cape Town
Not specified	EU513634.1	isolate CzanI1	SEA/RSA	Cape Town
voucher ADC09_261.9#9	JF493328.1_	-	SEA/RSA	Agulhas Bank
voucher ADC09_261.9#8	JF493327.1_	-	SEA/RSA	Agulhas Bank
voucher ADC09_261.9#7	JF493326.1_	-	SEA/RSA	Agulhas Bank
voucher ADC09_261.9#6	JF493325.1_	-	SEA/RSA	Agulhas Bank
Outgroups				
<i>Austroglossus microlepis</i> (Soleidae)				
voucher_USZAF_:09023	HM007674.1	-	-	-
voucher_USZAF_:09035	HM007675.1	-	-	-
voucher_USZAF_:09045	HM007676.1	-	-	-
voucher_USZAF_:09051	HM007677.1	-	-	-
voucher_USZAF_:09052	HM007678.1	-	-	-
<i>Austroglossus pectoralis</i>				

voucher_USZAF:GBA1	HM007679.1	-	-	-
voucher_USZAF_:GBA2	HM007680.1	-	-	-
voucher_USZAF_:GBA3	HM007681.1	-	-	-
voucher_USZAF_:RET30	HM007682.1	-	-	-
voucher_ADC09_262.35	JF492929.1	-	-	-
voucher_ADC09_262.36	JF492930.1	-	-	-
voucher_ADC09_262.37	JF492931.1	-	-	-
voucher_Smith_262.3_4	JF492932.1	-	-	-
voucher_Smith_262.3_1	JF492933.1	-	-	-
voucher_Smith_262.3_3	JF492934.1	-	-	-
Not specified	EU513715.1	isolate_ApecI1	-	-
Not specified	EU513716.1	isolate_ApecI2	-	-
Not specified	EU513717.1	isolate_ApecII1	-	-
<i>Bothus podas</i> (Bothidae)				
voucher_CSFOM-045	KJ709492.1	-	-	-
voucher_BoPo21N	KM538239.1	-	-	-
voucher_BoPo21B	KM538240.1	-	-	-
voucher_BoPo21F	KM538241.1	-	-	-
voucher_BoPo21A	KM538242.1	-	-	-
voucher_BoPo21X	KM538243.1	-	-	-
voucher_BoPo21D	KM538244.1	-	-	-
voucher_BoPo21E	KM538245.1	-	SEA/RSA	Agulhas Bank
voucher_BoPo21T	KM538246.1	-	SEA/RSA	Agulhas Bank
voucher_BoPo21U	KM538247.1	-	-	-
voucher_BoPo21V	KM538248.1	-	-	-
voucher_BoPo21S	KM538249.1	-	-	-
voucher_BoPo21Q	KM538250.1	-	-	-
voucher_BoPo21M	KM538251.1	-	-	-
voucher_BoPo21P	KM538252.1	-	-	-
voucher_BoPo21W	KM538253.1	-	-	-
voucher_BoPo21R	KM538254.1	-	-	-
voucher_BoPo21O	KM538255.1	-	-	-
voucher_BoPo21C	KM538256.1	-	-	-
voucher_1145	KY176409.1	-	-	-
Not specified	EU513619.1	isolate_BpodI2	-	-
Not specified	EU513620.1	isolate_BpodI3	-	-
Not specified	EU513621.1	isolate_BpodII1	-	-

Table A2. Diagnostic characters according to both syntypes (present data) and the illustrations of *C. senegalensis* as presented in some key scientific publications. For the illustrations themselves, see Figure A2 in Appendix B. Data on lectotype (lt *sen*) and paralectotype (plt *sen*) of *C. senegalensis* (based on the present study), of which the latter belongs to *C. simulator* (*sim*). References, in chronological order, are listed in Table A3 in Appendix A. Measurements, counts, and qualitative characteristics are defined in the M&M Section, or further details are given below. **Legend:** IOD/VED¹ (IOD in %VED): qualitative value (shorter, about equal or longer) of interorbital distance (IOD) in relation to vertical eye diameter (VED); IOD/VED² (IOD in %VED): quantitative value (%) of IOD in relation to VED with >: longer than, <: shorter than and ≈: about equal; data between brackets come from the text of the reference cited; mouth angle: position of mouth angle relative to posterior border of the lower eye; »: exceeding the level of the posterior border of the lower eye; «: not exceeding that level; and LL os/bs: number of lateral lines on ocular side (os) vs. on blind side (bs).

Nr	Characters	Syntypes		References				
		lt <i>sen</i>	plt <i>sen</i> (<i>sim</i>)	[32]	[40]	[11]	[69]	[22]
(i)	VED/HL	12.5%	8.2%	11.4% (8.3–12.5)%	(8–11%)	7.5 (5–9)%	11%	8%
(ii)	IOD/VED ¹	<	≈ (<)	> (<)	(>)	> (≈)	>	(≈)
	IOD/VED ²	50.6%	70.9%	90.0%	-	66.6%	136.3%	100%
(iii)	Mouth Angle	«	« (»)	» (-)	(« or »)	» (-)	«	»
(iv)	LL os/bs	2/os, 1/bs	2/os, 1/bs	2/os (2/os)	(2 or 3/os, 1 or 0/bs)	2/os (2/os)	2/os (2/os, 1/bs)	3/os (3/os)

Nr	Characters	Syntypes		References				
		lt <i>sen</i>	plt <i>sen</i> (<i>sim</i>)	[21]	[21]	[7]	[100]	[8]
				A	B			
(i)	VED/HL	12.5%	8.2%	11% (6–10%)	6.5%	10.5%	8%	9.3%
(ii)	IOD/VED ¹	<	<	≈ (≈)	>	≈ (>)	>	≈ (<)
	IOD/VED ²	50.6%	70.9%	62.5%	145.4%	-	150.6%	90.6%
(iii)	Mouth Angle	«	«	» (»)	»	« (»)	«	» (»)
(iv)	LL es/bs	2/os, 1/bs	2/os, 1/bs	2 (2 or 3)/os	2/os	2/os (2 or 3/os, 1/bs)	2/os (2/os, 1/bs)	2/os (2 or 3/os, 1/bs)

Table A3. References to illustrations and/or text data on diagnostic characters of *Cynoglossus senegalensis*.

Reference	Remark
[7]	Unknown locality and collector
[8]: 3039	Unknown locality and collector
[11]: figure 111bis	Collected in Lagos (Nigeria) by unknown collector
[21]: A. figure 14 and B. plate 2a and b	Drawing of specimen BMNH 1896.5.5.51 collected in the Ogowe River (Igowe), Lambaréné (Gabon) and photo of specimen USNM 247424 collected along the Lagos Coast (Nigeria)
[22]: figure 1110	Unknown locality and collector
[32]: figure 3	Illustrated specimen collected in Saint Louis (Senegal) by Paul Delhez
[40]: 203–204	Unknown locality and collector
[69]: figure 199	Collected in the Ebrié Lagoon (Cocody Bay, Ivory Coast) by Tournier and Briet
[100]: 369	Reprint 2011: 395 and also included in [19]: see figure 46.1, unknown locality and collector

Table A4. Overview of the references citing species of the economically most important fish families in the ECA. Publications: ● synthetic; * taxonomic paper. For details: (i) on the acronyms used for the different species, see Table A5 in Appendix A, and (ii) on the references, see SM: List S2.

Family/Sub-class		Tri-chi-uridae	Sciaenidae							Elasmobranchii																													Ariidae				Polynemidae			Cynoglossidae							
Nº		1.1	2.1	2.2	2.3	2.4	2.5	2.6	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8	3.9	3.10	3.11	3.12	3.13	3.14	3.15	3.16	3.17	3.18	3.19	3.20	3.21	3.22	3.23	3.24	3.25	3.26	3.27	3.28	3.29	4.1	4.2	4.3	5.1	5.2	5.3	6.1	6.2	6.3	6.4	6.5					
Species		Tl	Pe l	Pe p	Pmo	Pse	Pe	Pt	An	As	Av	Cal t	Cam b	Cbre	Cfal	Cleu	Clim	Cp	Csig	Pg	Ra	Cg	Cs qu	Dp	Fm	Gc	Io	Ip	Rmir	Rr	Rmar	Cc	Sl	Sz	Sb	Gg	Mm	Ch eu	Cl	Cpar	Gd	Pq	Pqu	Cb	Ccad	Ccan	Cm	Cs					
Nr	Publi-cations																																																				
	[101]	•																																																			
	[102]				*			•																																													
	[103]		•	•		•	•																																														
	[104]		•	•	•	•	•	•																																													
	[105]		*	*	*	*	*	*																																													
6	[106]									•	•	•	•	•	•	•	•	•	•	•	•	•	•				•	•					•	•	•	•	•	•															

[illegible]

1 9	$\begin{bmatrix} 1 \\ 19 \end{bmatrix}$																											*	*	*					
2 0	$\begin{bmatrix} 1 \\ 20 \end{bmatrix}$																											*	*	*					
2 1	$\begin{bmatrix} 1 \\ 21 \end{bmatrix}$																											•	•	•					
2 2	$\begin{bmatrix} 1 \\ 22 \end{bmatrix}$																											•	•	•					
2 3	$\begin{bmatrix} 1 \\ 23 \end{bmatrix}$																											*	*						
2 4	$\begin{bmatrix} 4 \\ 1 \end{bmatrix}$																														•	•			•
2 5	$\begin{bmatrix} 1 \\ 9 \end{bmatrix}$																																	•	
2 6	$\begin{bmatrix} 1 \\ 24 \end{bmatrix}$																														•				
2 7	$[8]$																														•	•	•	•	•
2 8	$[9 \atop 9]$																														*	*	*	*	*
2 9	$\begin{bmatrix} 1 \\ 25 \end{bmatrix}$																														•				
3 0	$\begin{bmatrix} 1 \\ 26 \end{bmatrix}$					•	•																							•				•	•

[illegible]

Table A5. Species list, with author(s) and date for each species and acronym used in Table A4 in Appendix A, of the economically most important fish families in the ECA. Families are listed according to economic importance, and species are listed alphabetically.

Nr	Acronym	Scientific Name	Author and Date	Subclass/Family
1.1	Tl	<i>Trichiurus lepturus</i>	Linnaeus, 1758	Trichiuridae
2.1	Pel	<i>Pseudolithus elongatus</i>	(Bowdich, 1825)	Sciaenidae
2.2	Pep	<i>Pseudolithus epipercus</i>	(Bleeker, 1863)	
2.3	Pmo	<i>Pseudolithus moorii</i>	(Günther, 1865)	
2.4	Ps	<i>Pseudolithus senegalensis</i>	(Valenciennes, 1833)	
2.5	PSl	<i>Pseudolithus senegallus</i>	(Cuvier, 1830)	
2.6	Pt	<i>Pseudolithus typus</i>	Bleeker, 1863	
3.1	An	<i>Aetobatus narinari</i>	(Euphrasen, 1790)	Elasmobranchii
3.2	As	<i>Alopias superciliosus</i>	(Lowe, 1841)	
3.3	Av	<i>Alopias vulpinus</i>	(Bonnaterre, 1788)	
3.4	Calt	<i>Carcharhinus altimus</i>	(Springer, 1950)	
3.5	Camb	<i>Carcharhinus amboinensis</i>	(Müller & Henle, 1839)	
3.6	Cbre	<i>Carcharhinus brevipinna</i>	(Valenciennes, 1839)	
3.7	Cfal	<i>Carcharhinus falciformis</i>	(Bibron, 1839)	
3.8	Cleu	<i>Carcharhinus leucas</i>	(Valenciennes, 1839)	
3.9	Clim	<i>Carcharhinus limbatus</i>	(Valenciennes, 1839)	
3.10	Cp	<i>Carcharhinus plumbeus</i>	(Nardo, 1827)	
3.11	Csig	<i>Carcharhinus signatus</i>	(Poey, 1868)	
3.12	Pg	<i>Prionace glauca</i>	(Linnaeus, 1758)	
3.13	Ra	<i>Rhizoprionodon acutus</i>	(Rüppell, 1837)	
3.14	Cg	<i>Centrophorus granulosus</i>	(Bloch & Schneider, 1801)	
3.15	Csqu	<i>Centrophorus squamosus</i>	(Bonnaterre, 1788)	
3.16	Dp	<i>Deania profundorum</i>	(Smith & Radcliffe, 1912)	
3.17	Fm	<i>Fontitrygon margarita</i>	(Günther, 1870)	
3.18	Gc	<i>Glaucostegus cemiculus</i>	(Geoffroy St. Hilaire, 1817)	
3.19	Io	<i>Isurus oxyrinchus</i>	Rafinesque, 1810	
3.20	Ip	<i>Isurus paucus</i>	Guitart Manday, 1966	
3.21	Rmir	<i>Raja miraletus</i>	Linnaeus, 1758	
3.22	Rr	<i>Rhinobatos rhinobatos</i>	(Linnaeus, 1758)	
3.23	Rmar	<i>Rhinoptera marginata</i>	(Geoffroy St. Hilaire, 1817)	
3.24	Cc	<i>Centroscymnus coelolepis</i>	Barbosa du Bocage & de Brito Capello, 1864	
3.25	Sl	<i>Sphyrna lewini</i>	(Griffith & Smith, 1834)	
3.26	Sz	<i>Sphyrna zygaena</i>	(Linnaeus, 1758)	
3.27	Sb	<i>Squalus blainville</i>	(Risso, 1827)	
3.28	Gg	<i>Galeorhinus galeus</i>	(Linnaeus, 1758)	
3.29	Mm	<i>Mustelus mustelus</i>	(Linnaeus, 1758)	
4.1	Cheu	<i>Carlarius heudelotii</i>	(Valenciennes, 1840)	Ariidae
4.2	Cl	<i>Carlarius latiscutatus</i>	(Günther, 1864)	
4.3	Cpar	<i>Carlarius parkii</i>	(Günther, 1864)	
5.1	Gd	<i>Galeoides decadactylus</i>	(Bloch, 1795)	Polynemidae
5.2	Pq	<i>Pentanemus quinquarius</i>	(Linnaeus, 1758)	
5.3	Pqu	<i>Polydactylus quadrifilis</i>	(Cuvier, 1829)	
6.1	Cb	<i>Cynoglossus browni</i>	Chabanaud, 1949	Cynoglossidae
6.2	Ccad	<i>Cynoglossus cadenati</i>	Chabanaud, 1947	
6.3	Ccan	<i>Cynoglossus canariensis</i>	Steindachner, 1882	

6.4	Cm	<i>Cynoglossus monodi</i>	Chabanaud, 1949
6.5	Cs	<i>Cynoglossus senegalensis</i>	(Kaup, 1858)

Table A6. Number of key publications since 2000 following [20] for the valid species of Cynoglossidae and the six most important fish families in the ECA according to available fisheries data (listed from most to least important) [14]. IUCN status: VU = Vulnerable, LC = Least Concern, NT = Near Threatened, EN = Endangered, DD = Data Deficient, = Not evaluated; Pub = number of publications, n = synthesising publications, * = taxonomic/biodiversity publications; Syn = number of synonyms; Rev = number of revalidations. For full details on which publication, which species and which publication is of taxonomic or synthetic nature, and for a full citation of the references used, see the SM: List S2, List of publications; for details on species, see Tables A4 and A5 in Appendix A.

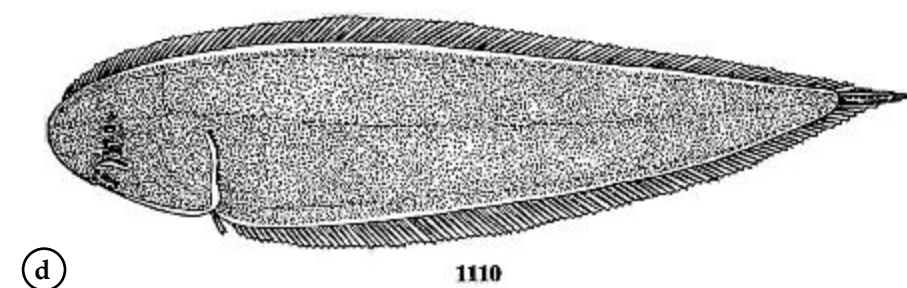
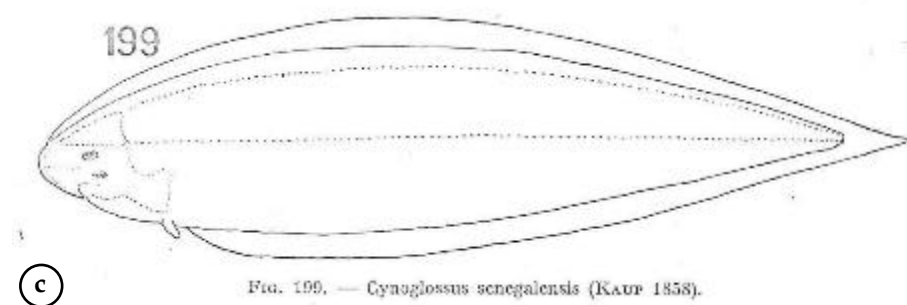
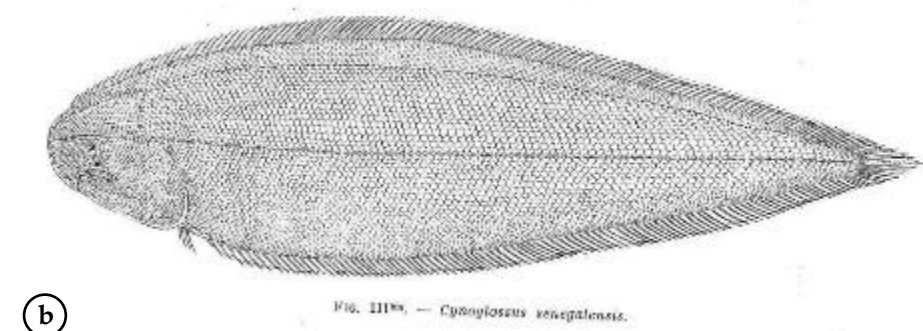
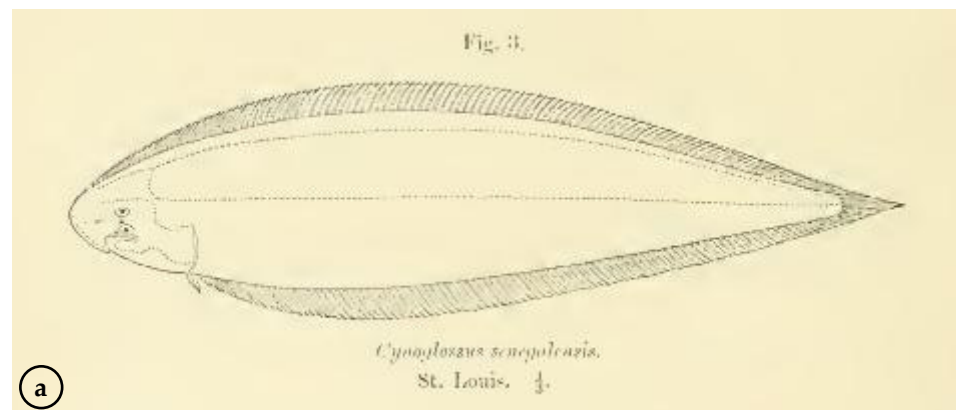
Nr	Subclass/Family	N	Species	IUCN status	Pub	Syn	Rev
1	Trichiuridae	1.1	<i>Trichiurus lepturus</i>	LC	1	0	0
			Total		1	0	0
2	Sciaenidae	2.1	<i>Pseudotolithus elongatus</i>	LC	6 (1 *)	4	0
		2.2	<i>P. epipercus</i>	LC	4 (1 *)	2	0
		2.3	<i>P. moorii</i>	LC	3 (1 *) + 1 (1 *)	2	0
		2.4	<i>P. senegalensis</i>	EN	5 (1 *) + 1	4	0
		2.5	<i>P. senegallus</i>	VU	5	2	0
		2.6	<i>P. typus</i>	LC	5 (1 *)	2	0
			Total		8 (2 *)	16	0
3	Elasmobranchii	3.1	<i>Aetobatus narinari</i>	EN	4	0	0
		3.2	<i>Alopias superciliosus</i>	VU	2	0	0
		3.3	<i>A. vulpinus</i>	VU	2	0	0
		3.4	<i>Carcharhinus altimus</i>	NT	2	0	0
		3.5	<i>C. amboinensis</i>	VU	2	0	0
		3.6	<i>C. brevipinna</i>	VU	3	0	0
		3.7	<i>C. falciformis</i>	VU	3	0	0
		3.8	<i>C. leucas</i>	VU	2	0	0
		3.9	<i>C. limbatus</i>	VU	3	0	0
		3.10	<i>C. plumbeus</i>	EN	2	0	0
		3.1	<i>C. signatus</i>	EN	2	0	0
		3.1	<i>Prionace glauca</i>	NT	3	0	0
		3.1	<i>Rhizoprionodon acutus</i>	VU	3	0	0
		3.1	<i>Centrophorus granulosus</i>	EN	2	0	0
		3.2	<i>C. squamosus</i>	EN	2	0	0
		3.2	<i>Deania profundorum</i>	NT	2	0	0
		3.2	<i>Fontitrygon margarita</i>	VU	4	0	0
		3.2	<i>Glaucostegus cemiculus</i>	CR	2	0	0
		3.2	<i>Isurus oxyrinchus</i>	EN	3	0	0
		3.20	<i>I. paucus</i>	EN	2	0	0
		3.2	<i>Raja miraletus</i>	LC	2	0	0
		3.2	<i>Rhinobatos rhinobatos</i>	CR	3	0	0
		3.2	<i>Rhinoptera marginata</i>	CR	3	0	0
		3.2	<i>Centroscyrnus coelolepis</i>	NT	2	0	0
		3.3	<i>Sphyrna lewini</i>	CR	3	0	0
		3.3	<i>S. zygaena</i>	VU	3	0	0
		3.3	<i>Squalus blainville</i>	DD	2	0	0
		3.3	<i>Galeorhinus galeus</i>	CR	2	0	0
		3.3	<i>Mustelus mustelus</i>	EN	1	0	0
			Total		4	0	0
4	Ariidae	4.1	<i>Carlarius heudelotii</i>	LC	1	0	0

		4.2	<i>C. latiscutatus</i>	LC	1	0	0
		4.3	<i>C. parkii</i>	LC	1+1	0	0
		Total			2	0	0
5	Polynemidae	5.1	<i>Galeoides decadactylus</i>	NT	12 (5 *)	4	0
		5.2	<i>Pentanemus quinquarius</i>	VU	8 (3 *)	3	0
		5.3	<i>Polydactylus quadrifilis</i>	LC	7 (2 *) + 3 (2 *)	1	0
		Total			15 (7 *)	8	0
6	Cynoglossidae	6.1	<i>Cynoglossus browni</i>	DD	6 (1 *)	0	0
		6.2	<i>C. cadenati</i>	DD	4 (1 *) + 1	2	1
		6.3	<i>C. canariensis</i>	NT	4 (1 *) + 1	1	1
		6.4	<i>C. monodi</i>	NT	5 (1 *) + 1	0	0
		6.5	<i>C. senegalensis</i>	NT	7 (1 *) + 2	3	2
		Total			11 (1 *)	6	4
Grand Total					37 (10 *)		

Appendix B



Figure A1. The lateral line on the blind side of the specimen of the holotype of *Cynoglossus browni* (MNHN 1949-023) from Dakar (Senegal) (220.0 mm SL).



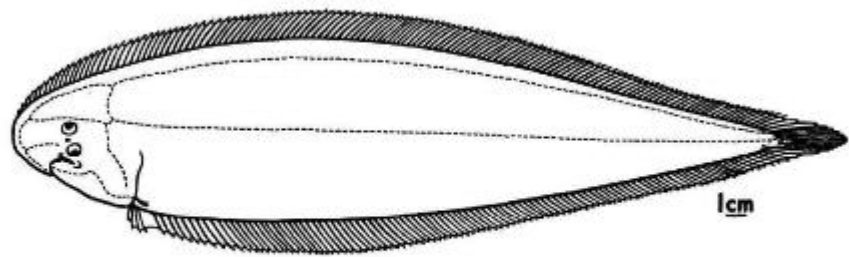
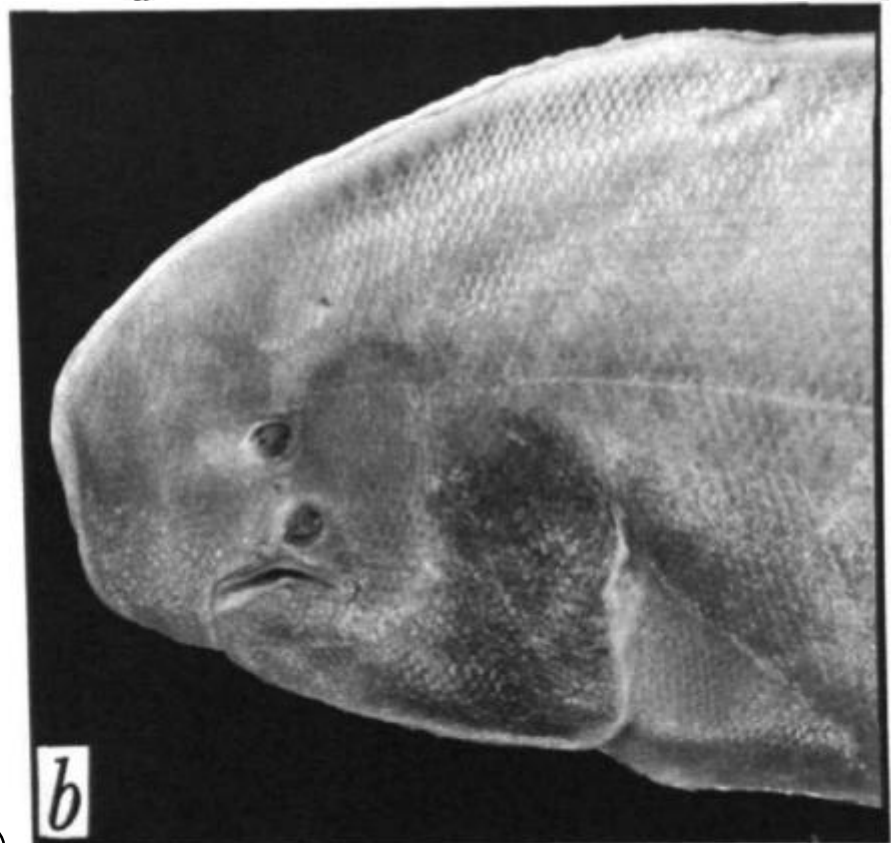


FIGURE 14.—Outline drawing of *C. senegalensis* (BMNH 1896.5.5.51) from Igowe River, Lambarene.

e



f



g

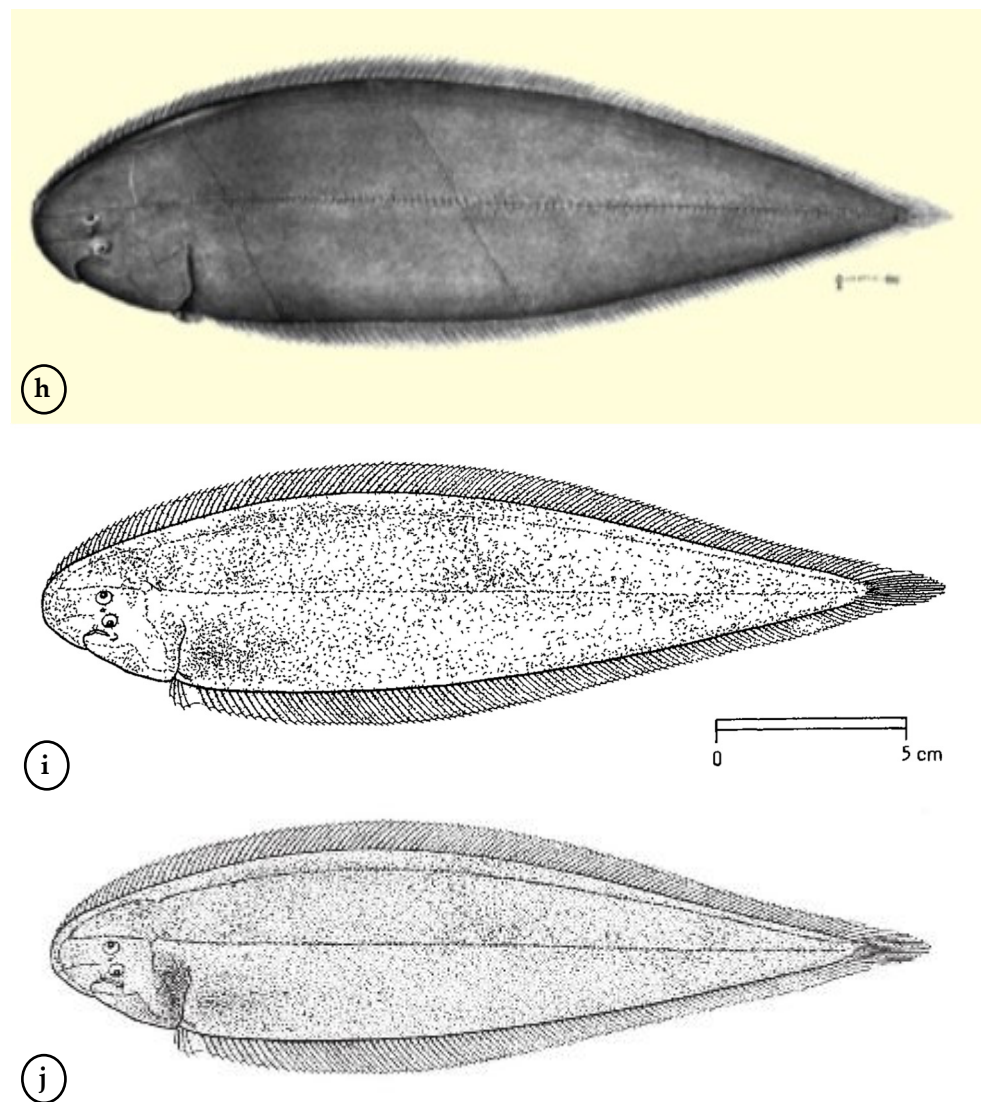


Figure A2. Key illustrations of *Cynoglossus senegalensis* as provided in the scientific literature: (a). Boulenger, 1916 [32]; (b). Poll, 1959 [11]; (c). Daget and Iltis, 1965 [69]; (d). Blache, Cadenat and Stauch, 1970 [22]; (e–g). Menon, 1977 [21]; (h). Séret and Opic, 1981 [100]; (i). Menon, 1981 [7]; and (j). Munroe, 2016 [8].



Figure A3. The third incomplete lateral line on the ocular side of the holotype of *Cynoglossus simulator* (see arrows) (MNHN 1949-022) from Sierra Leone (398.0 mm SL).

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