New insights into the systematics of fish genus *Gaidropsarus* (Gadiformes, Gadidae): flagging synonymies and hidden diversity

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Abstract

Gaidropsarus, Rafinesque 1810, is a genus of marine fishes, commonly known as rocklings, comprising 14 living species and showing a high ecological diversity from the intertidal zone to the deep sea. The systematics of this group has been controversial due to a general lack of representative specimens and the conservative morphology exhibited. A multidisciplinary approach combining the analysis of meristic data and the DNA barcode standard was applied in a species delimitation approach. Individuals representing eight valid and three unnamed species were collected, morphologically identified and archived in several museum collections. Comparison of DNA sequences shows complex results, furthering the idea of the difficult identification of specimens based on traditional taxonomy. DNA barcoding supports synonymies, like *G. biscayensis – G. macrophthalmus* and *G. guttatus – G. mediterraneus*, agreeing with the extensive overlaps observed in the meristic variables analysed and suggesting a reduction in the number of species. Genetic distances showed pairs of closely related species like *G. granti – G. vulgaris* and *G. argentatus – G. ensis*, the latter being only distinguished by one main distinctive character. Four deep-water specimens, morphologically classified only to the genus level, constituted three independent taxa apart from the ones present in this study and with no barcode matches in the repository databases. They could represent new records for the North Atlantic or unknown species of this genus. The results obtained show that more studies will be necessary to solve the systematics of this branch of the Gadiformes.

Keywords:
Barcoding, COI, Meristics, Morphology, Rocklings, Taxonomy

Introduction

The genus Gaidropsarus

The genus *Gaidropsarus* Rafinesque 1810 shows a remarkable ecological diversity and comprises 14 living species occurring from the intertidal zone to the deep-sea, from the arctic to temperate and subtropical waters. Eight of these species, *Gaidropsarus argentatus* (Reinhardt 1837), *Gaidropsarus biscayensis* (Collett 1890), *Gaidropsarus ensis* (Reinhardt 1837), *Gaidropsarus granti* (Regan 1903), *Gaidropsarus guttatus* (Collett 1890), *Gaidropsarus macrophthalmus* (Günther 1 867), *Gaidropsarus mediterraneus* (Linnaeus 1758) and *Gaidropsarus vulgaris* (Cloquet 1824) have been described in the North Atlantic Ocean and the Mediterranean Sea and they are still currently considered valid species.
Fishes from this genus, commonly known as rocklings, are characterised by an elongated and relatively slender body, with barbells present on the chin and at each

anterior nostril on the snout. The first dorsal ray is followed by a row of small fleshy filaments, the anal fin is not indented, and a lateral line is uninterrupted along its entire length (Cohen et al. 1990).
The classification of the species is controversial, having been alternatively placed in the family Gaidropsaridae (Howes, 1991; Iwamoto & Cohen 2016.), Gadidae (Endo, 2002; Teletchea *et al*. 2006; Roa-Varón & Ortí 2009; Nelson *et al*. 2016) and Lotidae (Van der laan *et al*. 2014; Froese & Pauly 2016). In its last edition, the reference compendium "Fishes of the World" (Nelson et al. 2016) places the genus *Gaidropsarus* in the family Gadidae, which is the criterion followed in this investigation.
In spite of the taxonomic revisions of rocklings published (de Buen 1934; Svetovidov 1948, 1986a, b; Iwamoto & Cohen 2016), it has been suggested that additional studies are needed. In fact, when morphology is compared to DNA data, discrepancies arise (Francisco et al., 2014). The lack of representative specimens of the known species in the collections of museums may account for the poor knowledge of the morphological variability in this genus (Balushkin, 2009).

DNA Barcoding

DNA barcoding has been considered an efficient aid to traditional taxonomy (Hebert & Gregory 2005; Savolainen et al., 2005), designed to facilitate fast and accurate identification of specimens from a short standardised DNA sequence (Hebert et al., 2003; Miller, 2007). In its strictest sense, DNA barcoding addresses only a limited aspect of the taxonomic process, by matching DNA sequences to "known" species, the latter being delimited with traditional (e.g. morphological) methodologies. In this context, the role of barcodes is to provide a methodology to assign unidentified specimens to already characterised species (Hebert et al., 2003). This is of great aid to the end users of taxonomy, and it is helping in making more rapid progress in identification of species and delimitation of species groups (Ratnasingham & Hebert 2007). However, where species are simply unknown or no attempts have been made to delimit them, the barcode approach as originally intended is inadequate in its applicability (Savolainen et al., 2005) and should be employed with precaution. It is generally assumed for most vertebrate species that it is possible to use DNA markers such as the mtDNA-COI to distinguish between species, and therefore the barcoding approach is based on the assumption that the variation within species of vertebrates is smaller than between species (Ratnasingham & Hebert 2007). As a consequence, DNA barcoding has the potential to aid taxonomic studies and help to clarify cases of potential synonymy (Bañón et al., 2013) and delimitation of cryptic species (Puckridge et al., 2013; Hyde et al., 2014). In order to infer species delimitations using mtDNA-COI, sequences need to take the following into consideration: retention of ancestral polymorphism, male-biased gene flow, selection on any mtDNA nucleotide, introgression following hybridisation, and paralogy resulting from the transfer of mtDNA gene copies to the nucleus (Moritz & Cicero 2004). Despite their benefits and pitfalls, the mtDNA-COI barcode sequences and their ever increasing taxonomic coverage have been considered an unprecedented resource for taxonomy and systematics studies and also, its function as a diagnostic tool must be kept open (Savolainen et al., 2005).
DNA barcoding is recognised as an important new tool that can be usefully applied to help resolve taxonomic issues in fishes based on the development of a reference library of barcode sequences from vouchered specimens (Ward et al., 2005; Ward et

al., 2009; Zemlak et al., 2009). The analysis of validated DNA barcodes for cluster recognition provides an efficient approach for recognising putative species (operational taxonomic units, OTU) (Kekkonen & Hebert 2014). The Barcode Index Number (BIN) system is a persistent registry for animal OTUs recognised through sequence variation in the mtDNA-COI barcode region (Ratnasingham & Hebert 2013).
On December 2016, a search of the BOLD database produced 45 specimen records of *Gaidropsarus* with barcodes comprising 5 species: *G. argentatus*, *G. ensis*, *G. mediterraneus*, *G. novazealandiae* and *G. vulgaris*, from which only 22 were public. A few DNA sequences of rocklings have been obtained and related to different attempts of inferring the phylogeny of gadiform fishes employing a variety of markers (Bakke & Johansen 2002, 2005; Teletchea et al., 2006; Von der Heyden & Matthee, 2008; Roa-Varón & Ortí 2009; Francisco et al., 2014) and with the molecular assignation of specimens employing the mt-COI barcode (Costa et al., 2012; McCuskey et al., 2013; Knebelsberger et al., 2014; Landi et al., 2014).
The aim of this investigation is to assign fish specimens of the genus *Gaidropsarus* found in the North Atlantic and the Mediterranean using DNA barcodes. To this end, a library combining sequences obtained from voucher specimens generated in this investigation and others of already deposited BOLD public records was built up. In order to understand the barcoding results, an extensive bibliographic revision of main distinctive morphological characters was carried out. In some cases, the comparison of sequences flags incongruity in the delimitation of species of this genus, characterised by a highly conserved morphology.

Material and Methods

Sample collection, morphological data and identification

Sampled at different locations in the North Atlantic and the Mediterranean were 149 specimens of rocklings (Fig. 1, Table S1). Specimens were captured in a variety of ecological niches, from shallow coastal waters (one specimen of *G. mediterraneus* at a depth of less than one metre in French Brittany) to deep waters (one specimen of *G. ensis* at a depth of 1,458 metres off Newfoundland and Labrador). Most specimens were immediately frozen and, upon transportation to the laboratory, muscle samples were removed and stored in 95% ethanol. In order to compare the available morphological data with the molecular results, an exhaustive bibliographical revision was carried out and is summarised in Table 1.
Specimens were identified to the species level according to Svetovidov (1986a, b). Vouchers were deposited in the "Muséum National d'Histoire Naturelle" (Concarneau and París, France), "Museo de Historia Natural da Universidade de Santiago de Compostela" (Santiago de Compostela, Spain) and "Colección de Fauna Marina del Centro Oceanográfico de Málaga" (CFM-IEOMA; Málaga, Spain). A project has been created in the BOLD database with the title "Molecular identification of *Gaidropsarus* fishes" (Code GSRUS) where data, including barcoding DNA sequences of specimens, photographs and other details are available. Sequences were also deposited in GenBank under Accession Numbers KY250169-KY250315, KY370533 and KY370534 (Table S1).

DNA extraction, PCR amplification and sequencing

Total DNA was purified from 25 mg of muscle tissue taken from each specimen according to the spin-column protocol of the Tissue DNA Extraction Kit (Omega-Biotek). The standard 5´ barcoding region of the COI gene (ca. 650 bp) was amplified by polymerase chain reaction (PCR) using the universal primer cocktail for fish DNA barcoding COI-3 (Ivanova et al., 2007). The following reaction conditions were applied: initial denaturation at 98 °C for 30 s followed by 35 cycles of 98 °C for 5 s, annealing at 52 °C for 5 s and 72 °C for 10 s, with a final extension at 72 °C for 1 min. PCR was carried out using Phire Green Hot Start II DNA Polymerase (Thermo Scientific); mixtures contained a final volume of 25 µl and included 12.5 µl of 2X Phire Green HS II PCR Master Mix, 2 µl of primer mixture and between 50 and 100 ng of template DNA. COI amplicon bands were visualised on 1.2% agarose gels (Seakem LE Agarose) stained with ethidium bromide and reactions were purified with ExoSAP-IT (Affymetrics) following the manufacturer´s instructions. DNA sequencing reactions were carried out in both senses using the M13F (-21) and M13R (-27) primers (Messing, 1983). The resulting products were resolved in an ABI3130 Genetic Analyser (Applied Biosystems, Foster City, CA, USA) and the consensus sequences were obtained after assembling the direct and reverse traces with SEQSCAPE v2.5 (Applied Biosystems).
Sequences of the 10 MNHN vouchers were obtained with the PCR primers S156/R249 or R084 and with the sequencing primers S165 (Iglésias et al., 2016).

Molecular analysis and assignment of specimens

A reference dataset was built with 149 mtDNA-COI sequences derived from voucher specimens assigned to *Gaidropsarus* species. They were aligned together with another 22 sequences retrieved from BOLD, employing the MUSCLE algorithm (Edgar, 2004). The specimens used in the analysis are listed in Tables S1 and S2 and comprise 171 barcodes. The criterion for the genetic divergence estimation was the number of base differences per site between sequences, also called uncorrected *p*-distance (Nei & Kumar 2000). Its use is more accurate for the intrageneric / intraspecific level estimations and yields higher or similar identification success rates for neighbour-joining trees than K2P distance, which overestimates the genetic distances (Srivathsan & Meier 2012). The molecular analysis was conducted using the Neighbor-Joining (NJ) method (Saitou & Nei 1987) in MEGA 6.0 (Tamura et al., 2013), with confidence limits tested through a bootstrap procedure (Felsenstein, 1985) with 2,000 replicates. The resulting tree was edited using TreeGraph 2 (Stöver & Müller 2010). A genetic distance matrix was obtained among the species-like clusters based on the molecular analysis in order to explore the data and detect possible specimen misidentifications or hybrids, as well as synonym or cryptic species.
The specimen assignment for every sequence was inferred from the existence of species-level assigned individuals belonging to the same cluster. In the absence of voucher specimens to compare with, specimen assignment was attempted using the identification tool present in BOLD Systems, which also allows comparison with private sequences. Sequences were grouped in representative haplotypes (Table S3) using the software DnaSP v5 (Librado & Rozas 2009).

Test of the proposed assignments

A comparison between the minimum distance value to a congener sequence with the maximum divergence within species was performed for each of the 171 barcodes, with the software TaxonDNA using *p*-distance (Meier et al., 2006).
Repeated values, from the same species, were represented only once and, therefore, a final scatterplot with 48 points was obtained. The distance-based species delimitation criteria formed four quadrants, representing one or more possible explanations for the assignments proposed: (I) Concordant with current taxonomy; (II) Cryptic species; (III) Recent divergence, Hybridization or Synonymy; (IV) Probable misidentification (Hubert & Hanner 2015). Two different sequence divergence values were used as criteria for the delimitation of species to establish the quadrants; 2%, as COI divergences rarely exceed this value within a named species and 3.9%, following the application of the "10x rule" for the data investigated in this case (Hebert et al., 2004; Ward et al., 2009).
The different values for the two criteria established a grey zone in the scatterplot in which the interpretation can vary.

Results

Meristic traits

Bibliographical data of the main distinctive characters of the nominal *Gaidropsarus* species are summarised in Table 1. An extensive overlap in the meristic variables analysed is observed, resulting in a set of conservative morphological traits. Regarding the two boreal species, *G. argentatus* and *G. ensis*, an overlap in the counts of all the characters is conspicuous. A similar result is obtained between *G. biscayensis* and *G. macrophthalmus* but to a lesser extent, with the second dorsal fin rays counts being in the range of 48-54 in the former, and 53-59 in the latter. On counting the anal fin rays, the ranges of *G. biscayensis* and *G. macrophthalmus* overlap slightly (40-46 vs 45-50). When *G. vulgaris* and *G. granti* are compared, the data collected from the literature referring to these main distinctive characters is unable to distinguish between the two species. In the case of the comparison between *G. mediterraneus* and *G. guttatus*, only the count of pelvic fin rays allows the distinction between both rocklings. In general, it can be said that the genus *Gaidropsarus* shows a highly conservative morphology.

NJ trees

The mtDNA-COI dataset comprised 171 DNA sequences, represented by 52 distinct haplotypes. The alignment contained 651 nucleotide positions from which 195 were variable and 180 parsimony-informative sites. One hundred and forty nine sequences of the reference dataset constituted new additions to the global library of published COI-5P barcodes for marine fish (Table S1).
The 52 haplotypes obtained produced a Neighbor-Joining tree (Figure 2) with nine clades. Most of them clustered haplotypes assigned to the same species, as is the case of *G. argentatus*, *G. ensis*, *G. granti*, *G. vulgaris* and the three unknown *Gaidropsarus* sp. 1, 2 and 3. Two other clades happened to be the result of the mixture of individuals assigned to two different species, *G. biscayensis* - *G. macrophthalmus* and *G. guttatus* - *G. mediterraneus.*
The NJ-analysis of the 171 sequences (Figure S1) showed that most of the 22 mt-COI sequences obtained from the public repositories clustered according to the species

assignation with few exceptions. Five *G. mediterraneus* sequences (JQ774626, KJ709762, KJ709763, KJ709764 and KP136735) are included in the *G. biscayensis* - *G. macrophthalmus* clade, one *G. vulgaris* sequence (SFM037-13) in the *G. guttatus* - *G. mediterraneus* clade and one *G. argentatus* sequence (KC015389) in the *G. ensis* clade. Therefore, seven out of 22 public sequences (31.81%) were assigned to misidentified specimens (Table S2).

Genetic distances

The within species mean distance was 0.39%, ranging from 0 to 1.38. The overall mean distance among the *Gaidropsarus* species was 11.40% (Table 2).
The between groups mean distances varied from 1.46% when comparing the clades formed by *G. granti* and *G. vulgaris* to 16.87% from *G. mediterraneus* - *G. guttatus* versus *Gaidropsarus* sp. 1. In general, they were well above 3%, with the exception of the two boreal species *G. argentatus* and *G. ensis*, which were closer (2.51%), and the comparisons of *G. vulgaris* and *G. granti* (1.46%). The genetic distances in the complex *G. biscayensis* - *G. macrophthalmus* ranged from 0 to 0.92% and from 0 to 1.1% for *G. guttatus* - *G. mediterraneus*. The within species mean distance observed was similar to the ones obtained for *G. argentatus* (0.58%) and *G. vulgaris* (0.56%) (Table 2). In general, the genetic distances observed showed the existence of a "Barcoding Gap", excepting the minor distance between *G. granti* and *G. vulgaris* (1.08%) which is lower than the highest within species value (1.38%) observed in *G. argentatus*. No relation between genetic distances and geographical locations was observed.
The representation of the highest within species value with the lowest between species value for every specimen showed that the majority of the comparisons lay within the recent divergence, hybridisation or synonymy quadrant III (Figure 3). As observed in the NJ tree, the individuals of species which clustered together showed the lowest between species divergence.
Even *G. granti* and *G. vulgaris*, which formed independent clades, fall into this category. The two boreal species, *G. argentatus* and *G. ensis*, are located in the overlapping zone between quadrant I and III. On the other hand, the individuals belonging to *Gaidropsarus* sp. 1 are located in quadrant I, concordant with well delimited species. The between species distance values of *Gaidropsarus* sp. 2 and 3 show that they are different species to the others consider in this investigation.

Assignment of unknown specimens

Four individuals were tentatively identified as *Gaidropsarus* sp. after morphological examination. The NJ tree analysis placed them in three independent clades, *Gaidropsarus* sp. 1, 2 and 3 respectively, distinct from the ones assigned to known species. The specimen identification requests performed through the BOLD identification tool yielded different results. The sequence KY250298 representing *Gaidropsarus* sp. 1 exhibited the highest similarity value (95.89%) with a sequence belonging to *G. novaezealandiae* (Hector, 1874), captured in the southern Atlantic Ocean (not of public access in BOLD). The sequence KY250299 named as *Gaidropsarus* sp. 2 showed the highest similarity value (92.40%) with several individuals of *G. argentatus*. The comparison of sequence KY370534 belonging to *Gaidropsarus* sp. 3, resulted in a similarity of 95.24% with the same sequence

as *Gaidropsarus* sp. 1. Curiously, these two species showed the highest similarity value with a South Atlantic sequence.

Discussion

General morphological traits

When the main meristic characters traditionally used as distinctive traits among *Gaidropsarus* are compared, the conspicuous overlaps observed in the measurements show that rocklings exhibit a conservative morphology, which hampers their identification based on traditional taxonomy. Original descriptions based only on a few specimens, and meristic and biometric data have been successively repeated since the pioneering work (Svetovidov, 1948) to the most recent (Iwamoto & Cohen 2016), without a critical revision. In the past, descriptions of new species were generally somewhat inconsistent, based on few specimens and morphological traits. Furthermore, the knowledge of the taxonomic status of fish species is unequal and clearly imbalanced in favour of coastal and/or commercial species, compared with the less known deep-water and/or non-commercial ones.

Gaidropsarus guttatus - Gaidropsarus mediterraneus

G. guttatus was described as a new species by the comparison of several morphological characters although its similarity with *G. mediterraneus* had already been reported when the holotype was described (Collett, 1890). Further investigations declared that the *G. guttatus* form was close, if not identical, to *G. mediterraneus* (Svetovidov, 1948). Recently, it has been stated that both species can be distinguished by the number of anal fin rays and their colour patterns (Iwamoto & Cohen 2016). However, the bibliographical revision of the meristic counts increases the number of anal fin rays invalidating it as a diagnostic character. The colour pattern can also be discarded as a taxonomical character due to its high variability among rocklings (Cohen & Russo 1979). *G. guttatus* and *G. mediterraneus* have a similar habitat consisting of intertidal pools and shallow waters, where the ecosystem is highly variable and a cryptic coloration suppose an adaptive advantage. The fact that the former species exhibits a darker colour pattern could probably correspond to an adaptation to the tones of the volcanic sea bed in the Macaronesian islands.

Despite *G. guttatus* bieing considered an endemic species of the Azores, Madeira and Canaries archipelagos (Avila et al., 2014). The majority of the Azorean marine biota seems to comprise species that have arrived predominantly from the Eastern Atlantic, especially from the region between southern Europe and northern Africa, and from the Mediterranean, where *G. mediterraneus* is distributed (Morton & Britton 2000). According to this, the hypothesis of a colonisation by *G. mediterraneus* of the Azores islands cannot be discarded.

The genetic distances between these two nominal species fall within the typical intraspecific values measured in marine fishes (Ward et al., 2009). Different hypothesis could explain these results, such as recent divergence, hybridisation, synonymy or misidentification of specimens, the latter being the first to be considered when COI sequence comparisons show incongruent results. In this case, this is unlikely since these two species could easily be distinguished, either by the coloration and/or distribution

(Svetovidov, 1986 a,b). A hybridisation event between both species cannot be rejected using only a mitochondrial marker (Savolainen et al., 2005). Here, the absence of shared distribution areas argues against this possibility. Nevertheless, the analysis of nuclear markers would be necessary to discard this hypothesis.
DNA barcoding results argue in favour of a synonymy and, although morphological data and distribution areas do not disagree with the former idea, they highlight the existence of a possible population structure or speciation process. The analysis of more rapidly evolving DNA markers, as microsatellites, would be needed in order to test the latter hypothesis.

Gaidropsarus biscayensis - Gaidropsarus macrophthalmus

In its description as a new species, it was stated that *G. biscayensis* could be distinguished from the similar *G. macrophthalmus* by a smaller head and different coloration and dentition (Collett, 1905). According to a recent revision (Iwamoto & Cohen 2016), which does not change the values reported by the reference one (Svetovidov 1986a), both species can be distinguished by the number of second dorsal fin rays and by the number of anal fin rays. The bibliographic revision of the meristic counts slightly overlaps the second dorsal and the anal fin ranges, discarding these characters as distinctive.
The description of both species also takes into account their separated distribution ranges, with *G. biscayensis* having a southern distribution from the Iberian Peninsula south to Morocco (24°N) and Madeira, and also from the western Mediterranean, Adriatic and Aegean Seas, whereas *G. macrophthalmus* ranges from the Faeroe Islands towards the south along the west coast of the British Isles to the Bay of Biscay and even to the south of the Azores Islands (Svetovidov, 1986a; Cohen et al., 1990; Iwamoto & Cohen 2016). However, *G. macrophthalmus* has been also reported south of this area, in Galician waters (Bañón et al., 2010) and in Portugal (Carneiro et al., 2014). The identification of several *G. macrophthalmus* specimens in the western Mediterranean discards the distribution area as a criterion to differentiate both species. Molecular results suggest the existence of a unique species with an Atlantic-Mediterranean distribution, as occurs in the cases of *G. mediterraneus*, *G. vulgaris* and *G. granti*. Contrary to what was widely believed, the Gibraltar sill is not an impenetrable barrier for fishes and a certain number of species endemic to the Mediterranean Sea have also been captured in the Atlantic Ocean or made synonyms of Atlantic species (Danovaro et al., 2010). For example, barcoding data together with morphological analysis shows a synonymy between the Atlantic *Lepidion eques* (Günther 1887) and the Mediterranean *Lepidion lepidion* (Risso 1810) morids, resulting in the latter being the only valid species with an Atlantic and Mediterranean distribution (Bañón et al., 2013; Barros-García et al., 2016).
Moreover, some morphological differences found among Atlantic and Mediterranean specimens of the same species can be attributed to their size, shown to be larger in the Atlantic Ocean (Massutí et al., 2004), and to geographical variations related to different environmental conditions, mainly temperature (Barlow, 1961; Bañón et al., 2013).
All the individuals assigned to *G. biscayensis* and *G. macrophthalmus* grouped together in the same cluster. Different explanations could account for this result, including specimen misidentification, synonymy or hybridization events. The latter, could be

favour by the existence of an overlap in their distribution areas between these two species, as occurs in the western Mediterranean. The large number of individuals sampled in their distribution areas, makes hybridisation processes or misidentification unlikely.
Since information in literature is restricted to but a few individuals, the morphological diversity could have being underestimated. Therefore, a further sampling is required in order to describe real distinctive traits, which would possibly show an overlap in the morphological data, agreeing with the barcoding and suggesting that *G. biscayensis* is a junior synonym of *G. macrophthalmus*.

Low genetic divergence between Gaidropsarus granti and Gaidropsarus vulgaris

G. granti was first described by Regan (1903) based on a specimen caught in the Azores Islands. It is a little known species, with few specimens described in literature. Although it was believed that this rockling was only distributed in the Azores and the Canary Islands (Svetovidov, 1986b), recent records have also found this species in different areas of the Atlantic and the Mediterranean (García, 2015). Morphological analysis pointed out *G. granti* as a species close to *G. mediterraneus* and *G. guttatus* (Svetovidov, 1986a), although molecular data show that it is closer to *G. vulgaris*, from which it differs mainly in its coloration pattern, habitat and distribution. *G. vulgaris* is a common species found on the continental shelf up to a depth of 120 m and is characterised by the presence of numerous dark spots (Svetovidov, 1986b). Meanwhile, *G. granti* is a rare species mainly distributed on seamounts and islands between depths of 120 to 830 m and with a characteristic white stripe on the body (García, 2015).
In DNA barcoding, species delimitation depends on the cut-off value employed, able to distinguish within species diversity from between species divergence (Ward et al., 2009). Different criteria have been proposed from which the "10x rule" implies that two sequences with a divergence higher than 10 times the average within species value could be considered as belonging to different species (Hebert et al., 2004). Lately, after surveying more than 1000 species of marine fish, it was stated that two barcodes with a 2% COI divergence value show a conspecific probability of only 3% (Ward et al., 2009). The combination of both criteria defines a 2%-3.9% range in which species delimitation would be uncertain.
The results obtained in the distances scatterplot between *G. granti and G. vulgaris* show that all the values are under 2%, falling in the zone where hybridisation, synonymy or recent divergence are possible. Despite this fact, these specimens form independent clades concordant with current taxonomy in the NJ analysis making hybridisation phenomena unlikely. Nevertheless, more individuals of *G. granti* and the use of nuclear markers would be necessary in order to discard this hypothesis.
Taking into account all the available data, it would appear that *G. granti* and *G. vulgaris* are two valid but closely related species.

Low genetic divergence between G. argentatus and *G. ensis*

These two boreal species are separated by low genetic distances, with the smallest value being 2%, a fact also observed in an Atlantic marine fishes study in Canada (McCusker et al., 2012). Depending upon the criterion put into practise to delimitate species, the results may vary. Considering the 2% criterion, both species are concordant with current taxonomy, but taking into account the 10x rule, which yields a

cut-off value of 3.9%, the relationship between them could be explain as the result of recent divergence, synonymy or hybridisation. The latter can be discarded considering the sampling carried out and the existence of two well-defined clusters, each one representing one of the species. The length of the first dorsal fin ray and the presence/absence of a median supratemporal pore, clearly distinguish both species morphologically (Cohen & Russo 1979; Svetovidov, 1986 a,b), making synonymy unlikely. Therefore *G. argentatus* and *G. ensis* should be considered two closely related valid species.

Unidentified specimens

Four specimens were captured in the eastern North Atlantic, between depths of 500 and 1230 m. Despite the fact that this study deals with all the recognised species from North Atlantic and Mediterranean, their barcodes branched into three independent clusters and were, therefore, named as *Gaidropsaru*s sp. 1, 2 and 3. Two possibilities arise from these results, new records of previously recognised southern species in the North Atlantic or the discovery of new deep-water species. In any case, these findings reflect the general lack of knowledge of the deep-sea environments even in such well characterised areas as the North Atlantic Ocean and the Mediterranean Sea (UNEP, 2006).

Misidentified public records

The comparison of newly generated barcodes with published data may help to detect misidentifications, taxonomic uncertainties or real cases of haplotype sharing among species (Knebelsberger & Thiel 2014). In this study, the comparison between a self-created barcoding database, curated by expert taxonomists, with all publically available sequences deposited in the repositories has flagged the presence of several misidentifications of *Gaidropsarus* voucher records in the latter. Most of the misidentifications found in the repository databases are related to the construction of DNA barcode reference libraries where only one sequence was employed and not compared with other *Gaidropsarus* barcodes (Costa et al., 2012; Landi et al., 2014; Knebelsberger et al., 2014).
Indeed, accumulating FISH-BOL data suggest that initial specimen misidentification appears to be considerably more worrying than complications caused by hybridisation (Ward et al., 2009). This fact can have serious implications for end users of reference libraries and once a name has been added to a database, it may be difficult for a third party to convince data managers that it should be changed (Collins & Cruickshank 2013).

Final remarks

The results of this investigation suggest that morphology-based identification and taxonomy can be challenging in *Gaidropsarus*, even within regions as well characterised as the North Atlantic Ocean and the Mediterranean Sea, and have highlighted the need for further detailed taxonomic examinations of this genus. In some species, the apparent contradictions between molecular and morphological data could be explained by the low number of individuals examined, with countable traits difficult to distinguish. This lack of sampling could lead to underestimations in the

morphological variability showing false distinctive values in their meristic. Therefore, an updated identification key of rocklings, based on increased sampling sizes and broader geographical areas is required to reflect their real morphological variability. DNA Barcoding can be used to distinguish *Gaidropsarus* species with a high degree of accuracy with some exceptions related to its challenging systematics and complex evolutionary history. The high contribution in number of specimens and diversity of species, and the detection of misidentifications in the public repositories, could make the task for future investigations of this genus easier.

The results suggest a more complex evolutionary history than expected, with low genetic distances observed between pairs of species that are morphologically distinguishable, which could be explained by recent or on-going speciation processes. What is more, the fact that COI-sequences obtained from unknown deep-water specimens are more similar to a South Atlantic record, despite their collection site, could suggest a connection between northern and southern hemisphere species. The impossibility of species-level assignation of four specimens captured in deep-water environments highlights the general lack of knowledge of these ecosystems. Furthermore, these results show that the existence of different and little known types of deep habitats could hold an undetermined number of new *Gaidropsarus* species.

An integrative taxonomy approach, considering not only morphology and barcoding, but also phylogeography, population genetics, ecology, development and behaviour could be necessary to delineate correct species boundaries in this genus.

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Legends to figures:

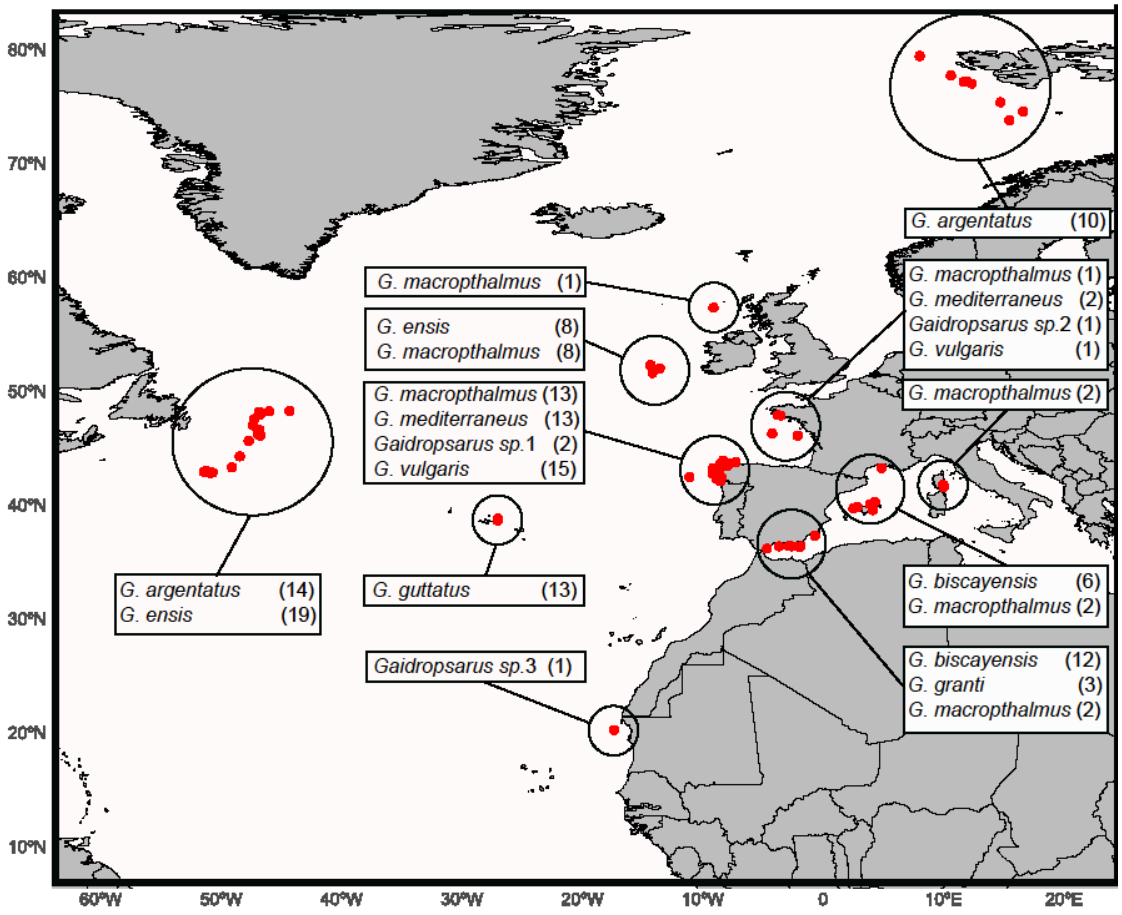
Figure 1. Sampling areas of *Gaidropsarus* in the North Atlantic Ocean and in the Mediterranean Sea, including species captured and number of specimens (shown in brackets).

Figure 2. Neighbor-Joining tree of COI haplotypes of *Gaidropsarus* fishes based on *p*-distances. Numbers at the main nodes are bootstrap percentages after 2000 replicates. Only values higher than 70% are shown. Subtrees include species assignations.

Figure 3. Scatterplot of maximum within species distances compared to minimum between species distances. Two different cut-off values were chosen to discriminate among species, the 2% criteria and the 10x rule. This creates a grey area where the delimitation is unclear and depends on the criterion selected. The graph is also divided into four quadrants representing different categories: (I) Concordant with current taxonomy; when the value of maximum within species distance is below the cut-off and the minimum between species distance is above the cut-off. (II) Cryptic species; when both distances are above the cut-off value selected. (III) Recent divergence, hybridisation or synonymy; when both distances are under the cut-off value. (IV) Probable misidentification; when the maximum within species distance is above the cut-off and the minimum between species distance is under the cut-off.

Data accessibility

Photographs, DNA sequence data and other details of the reference dataset of specimens employed in this investigation are available in the Barcode of Life Database in the project entitled "Molecular identification of *Gaidropsarus* fishes", code GSRUS. Barcodes have also been deposited in GenBank under accession numbers KY250169-KY250315, KY370533 and KY370534.


80°N
70°N
60°N
50°N
40°N
30°N
20°N
10°N
60°W
50°W
40°W
30°W
20°W
10°W
0
10°E
20°E
G. argentatus (10)
G. macropthalmus (1)
G. mediterraneus (2)
Gaidropsarus sp.2 (1)
G. vulgaris (1)
G. macropthalmus (1)
G. ensis (8)
G. macropthalmus (8)
G. macropthalmus (13)
G. mediterraneus (13)
Gaidropsarus sp.1 (2)
G. vulgaris (15)
G. macropthalmus (2)
G. argentatus (14)
G. ensis (19)
G. guttatus (13)
G. biscayensis (6)
G. macropthalmus (2)
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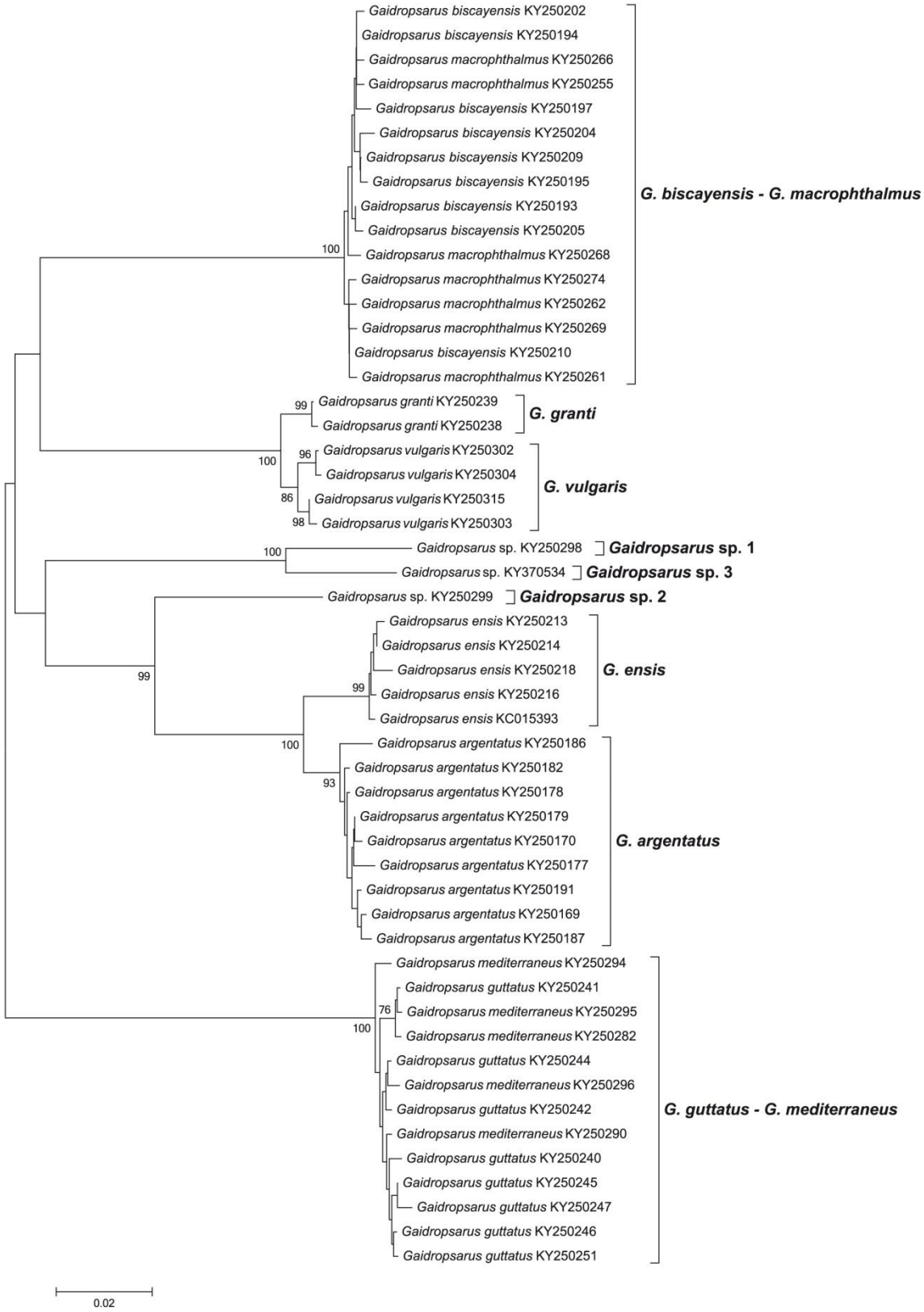
G. biscayensis (12)
G. granti (3)
G. macropthalmus (2)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Gaidropsarus biscayensis KY250204
Gaidropsarus biscayensis KY250209
Gaidropsarus biscayensis KY250195
Gaidropsarus biscayensis KY250193
Gaidropsarus biscayensis KY250205
Gaidropsarus macrophthalmus KY250268
Gaidropsarus macrophthalmus KY250274
Gaidropsarus macrophthalmus KY250262
Gaidropsarus macrophthalmus KY250269
Gaidropsarus biscayensis KY250210
Gaidropsarus macrophthalmus KY250261
G. biscayensis - G. macrophthalmus
Gaidropsarus granti KY250239
Gaidropsarus granti KY250238
G. granti
Gaidropsarus vulgaris KY250302
Gaidropsarus vulgaris KY250304
Gaidropsarus vulgaris KY250315
Gaidropsarus vulgaris KY250303
G. vulgaris
Gaidropsarus sp. KY250298
Gaidropsarus sp. 1
Gaidropsarus sp. KY370534
Gaidropsarus sp. 3
Gaidropsarus sp. KY250299
Gaidropsarus sp. 2
Gaidropsarus ensis KY250213
Gaidropsarus ensis KY250214
Gaidropsarus ensis KY250218
Gaidropsarus ensis KY250216
Gaidropsarus ensis KC015393
G. ensis
Gaidropsarus argentatus KY250186
Gaidropsarus argentatus KY250182
Gaidropsarus argentatus KY250178
Gaidropsarus argentatus KY250179
Gaidropsarus argentatus KY250170
Gaidropsarus argentatus KY250177
Gaidropsarus argentatus KY250191
Gaidropsarus argentatus KY250169
Gaidropsarus argentatus KY250187
G. argentatus
Gaidropsarus mediterraneus KY250294
Gaidropsarus guttatus KY250241
Gaidropsarus mediterraneus KY250295
Gaidropsarus mediterraneus KY250282
Gaidropsarus guttatus KY250244
Gaidropsarus mediterraneus KY250296
Gaidropsarus guttatus KY250242
Gaidropsarus mediterraneus KY250290
Gaidropsarus guttatus KY250240
Gaidropsarus guttatus KY250245
Gaidropsarus guttatus KY250247
Gaidropsarus guttatus KY250246
Gaidropsarus guttatus KY250251
G. guttatus - G. mediterraneus
100
99
96
100
86
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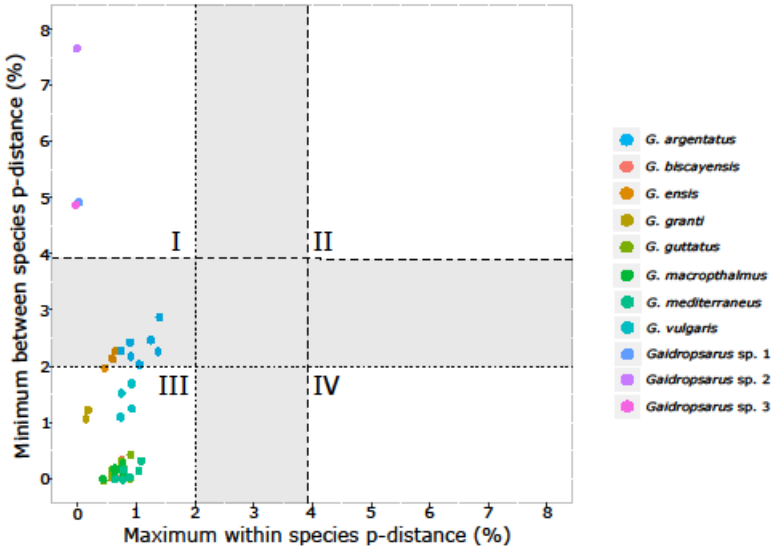
76
100
0.02


Minimum between species p-distance (%)
Maximum within species p-distance (%)
I
II
III
IV
0
1
2
3
4
5
6
7
8
G. argentatus
G. biscayensis
G. ensis
G. granti
G. guttatus
G. macrophthalmus
G. mediterraneus
G. vulgaris
Gaidropsarus sp. 1
Gaidropsarus sp. 2
Gaidropsarus sp. 3

	Vertebrae	2nd D-fin rays	A-fin rays	V-fin rays	P-fin rays	Gill rakers	Source
G. argentatus	49–53	52–65	43–51	7–8	22–24	1+8-11	4,5,6,10
G. ensis	50–54	52–64	40–48	6–7	20–27	1–2+10–11	4,5,6,10
G. biscayensis	43–47	48–54	40–46	6–7	18–20	+6–7	5,6,13
G. macrophthalmus	45–47	53–59	45–50	6–7	17–19	+8–9	5,6,13
G. vulgaris	46–49	56–64	46–54	6–7	21–22	+7–9	5,6,13
G. granti	47	55-60	45–52	7–8	20–22	1+9	1,5,6,7,8,9,11,12
G. guttatus	47–50	48–58	42–50	7	16–19	+7–9	2,3,5,13
G. mediterraneus	46–50	51–63	44–52	5–6	16–19	+7–10	5,6,13

Table 1: Counts of the main distinctive characters of *Gaidropsarus* species from the north Atlantic and Mediterranean. Species was ordered from up to down by similar species pair according to barcoding results. Sources: 1=Regan (1903); 2= Svetovidov (1948); 3= Maul (1952); 4= Marckle (1982); 5= Svetovidov (1986a); 6= Svetovidov (1986b); 7= Zachariou-Mamalinga (1999); 8= Bañón et al. (2002); 9= Mura & Cau (2003); 10= Fahay (2007); 11= Pais et al. (2008); 12= Orsi-Relini & Relini (2014); 13= Cohen & Iwamoto (2016). Abreviatures: Dorsal (D), Anal (A), Pelvic (V) and Pectoral (P)

Table 2. Mean nucleotide distance (% of *p*-distance) within and between species of *Gaidropsarus* (range values shown in brackets).

		Between species							
Species[1] (n)	Within sp.	Gar	Gbi-Gma	Gen	Ggr	Ggu-Gme	Gvu	Gsp1	Gsp2
Gar (29)	0.58 (0-1.38)								
Gbi-Gma (47)	0.51 (0-0.92)	14.51 (13.98-14.90)							
Gen (34)	0.37 (0-0.61)	2.51 (2.00-3.07)	14.89 (14.44-15.05)						
Ggr (3)	0.15 (0-0.15)	13.08 (12.75-13.36)	12.37 (11.98-12.60)	13.96 (13.67-14.29)					
Ggu-Gme (33)	0.58 (0-1.1)	14.76 (14.59-15.05)	15.69 (15.05-16.28)	15.03 (14.59-15.67)	15.24 (14.75-15-67)				
Gvu (21)	0.56 (0-0.92)	13.17 (12.90-13.52)	12.43 (11.98-12-90)	14.04 (13.67-14.44)	1.46 (1.08-1.84)	15.01 (14.44-15-21)			
Gsp1 (2)	0	13.69 (13.36-14.13)	15.75 (15.36-16.13)	14.16 (14.13-14.44)	13.29 (13.21-13.36)	16.87 (16.59-17.36)	14.13 (13.98-14.29)		
Gsp2 (1)	-	7.95 (7.68-8.29)	13.58 (13.21-13.82)	8.08 (7.83-8.29)	12.06 (11.98-12.14)	14.65 (14.44-14.90)	12.90 (12.75-13.06)	12.90	
Gsp3 (1)	-	13.98 (13.67-14.29)	14.83 (14.44-15.05)	14.62 (14.44-14.90)	13.59 (13.52-13.67)	16.32 (15.82-16.59)	14.06 (13.98-14.13)	4.92	13.67

[1]Gar: *Gaidropsarus argentatus*; Gbi-Gma: *Gaidropsarus biscayensis-Gaidropsarus macrophthalmus*, Gen: *Gaidropsarus ensis*; Ggr: *Gaidropsarus granti*; Ggu-Gme: *Gaidropsarus guttatus-Gaidropsarus mediterraneus*; Gvu: *Gaidropsarus vulgaris*; Gsp1: *Gaidropsarus* sp. 1; Gsp2: *Gaidropsarus* sp. 2; Gsp3: *Gaidropsarus* sp. 3.

Table S1. North Atlantic and Mediterranean *Gaidropsarus* reference dataset (n = 149)

Morphological identification	Region	BOLD Process ID	GB Accession No.
Gaidropsarus argentatus	Barents Sea	GDT001	KY250179
Gaidropsarus argentatus	Barents Sea	GDT002	KY250169
Gaidropsarus argentatus	Barents Sea	GDT003	KY250192
Gaidropsarus argentatus	Barents Sea	GDT004	KY250191
Gaidropsarus argentatus	Barents Sea	GDT005	KY250190
Gaidropsarus argentatus	Barents Sea	GDT006	KY250189
Gaidropsarus argentatus	Barents Sea	GDT008	KY250188
Gaidropsarus argentatus	Barents Sea	GDT009	KY250187
Gaidropsarus argentatus	Barents Sea	GDT010	KY250186
Gaidropsarus argentatus	Barents Sea	GDT011	KY250185
Gaidropsarus argentatus	Newfoundland and Labrador	GDT012	KY250184
Gaidropsarus argentatus	Newfoundland and Labrador	GDT013	KY250183
Gaidropsarus argentatus	Newfoundland and Labrador	GDT014	KY250182
Gaidropsarus argentatus	Newfoundland and Labrador	GDT015	KY250181
Gaidropsarus argentatus	Newfoundland and Labrador	GDT016	KY250180
Gaidropsarus argentatus	Newfoundland and Labrador	GDT017	KY250177
Gaidropsarus argentatus	Newfoundland and Labrador	GDT020	KY250176
Gaidropsarus argentatus	Newfoundland and Labrador	GDT021	KY250175
Gaidropsarus argentatus	Newfoundland and Labrador	GDT022	KY250174
Gaidropsarus argentatus	Newfoundland and Labrador	GDT023	KY250173
Gaidropsarus argentatus	Newfoundland and Labrador	GDT024	KY250172
Gaidropsarus argentatus	Newfoundland and Labrador	GDT025	KY250171
Gaidropsarus argentatus	Newfoundland and Labrador	GDT026	KY250170
Gaidropsarus argentatus	Newfoundland and Labrador	GDT027	KY250178
Gaidropsarus biscayensis	Andalucía	GGY002	KY250210
Gaidropsarus biscayensis	Andalucía	GGY003	KY250193
Gaidropsarus biscayensis	Andalucía	GGY004	KY250209
Gaidropsarus biscayensis	Balearic Islands	GGY005	KY250208
Gaidropsarus biscayensis	Andalucía	GGY006	KY250207
Gaidropsarus biscayensis	Balearic Islands	GGY007	KY250206
Gaidropsarus biscayensis	Balearic Islands	GGY008	KY250205
Gaidropsarus biscayensis	Balearic Islands	GGY009	KY250204
Gaidropsarus biscayensis	Balearic Islands	GGY010	KY250203
Gaidropsarus biscayensis	Andalucía	GGY011	KY250202
Gaidropsarus biscayensis	Andalucía	GGY012	KY250201
Gaidropsarus biscayensis	Andalucía	GGY013	KY250200
Gaidropsarus biscayensis	Andalucía	GGY014	KY250199
Gaidropsarus biscayensis	Andalucía	GGY015	KY250198

Gaidropsarus biscayensis	Andalucía	GGY016	KY250197
Gaidropsarus biscayensis	Andalucía	GGY017	KY250196
Gaidropsarus biscayensis	Andalucía	GGY018	KY250195
Gaidropsarus biscayensis	Balearic Islands	GGY019	KY250194
Gaidropsarus ensis	Flemish Cap	GDE001	KY250213
Gaidropsarus ensis	Flemish Cap	GDE002	KY250214
Gaidropsarus ensis	Flemish Cap	GDE003	KY250215
Gaidropsarus ensis	Flemish Cap	GDE004	KY250216
Gaidropsarus ensis	Flemish Cap	GDE005	KY250217
Gaidropsarus ensis	Flemish Cap	GDE006	KY250218
Gaidropsarus ensis	Flemish Cap	GDE007	KY250219
Gaidropsarus ensis	Flemish Cap	GDE009	KY250220
Gaidropsarus ensis	Newfoundland and Labrador	GDE010	KY250211
Gaidropsarus ensis	Newfoundland and Labrador	GDE011	KY250228
Gaidropsarus ensis	Newfoundland and Labrador	GDE012	KY250222
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Gaidropsarus ensis	Newfoundland and Labrador	GDE015	KY250225
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Gaidropsarus ensis	Newfoundland and Labrador	GDE017	KY250227
Gaidropsarus ensis	Newfoundland and Labrador	GDE018	KY250221
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Gaidropsarus ensis	Newfoundland and Labrador	GDE064	KY250235
Gaidropsarus ensis	Newfoundland and Labrador	GDE065	KY250236
Gaidropsarus ensis	Newfoundland and Labrador	GDE066	KY250237
Gaidropsarus ensis	Newfoundland and Labrador	GDE067	KY250212
Gaidropsarus granti	Andalucía	GGA001	KY250239
Gaidropsarus granti	Andalucía	GGA002	KY250238
Gaidropsarus granti	Andalucía	GGA003	
Gaidropsarus guttatus	Azores Islands	GGT001	KY250240
Gaidropsarus guttatus	Azores Islands	GGT002	KY250241
Gaidropsarus guttatus	Azores Islands	GGT003	KY250242
Gaidropsarus guttatus	Azores Islands	GGT004	KY250243
Gaidropsarus guttatus	Azores Islands	GGT005	KY250244
Gaidropsarus guttatus	Azores Islands	GGT006	KY250245

Gaidropsarus guttatus	Azores Islands	GGT007	KY250246
Gaidropsarus guttatus	Azores Islands	GGT008	KY250247
Gaidropsarus guttatus	Azores Islands	GGT009	KY250248
Gaidropsarus guttatus	Azores Islands	GGT010	KY250249
Gaidropsarus guttatus	Azores Islands	GGT011	KY250250
Gaidropsarus guttatus	Azores Islands	GGT012	KY250251
Gaidropsarus guttatus	Azores Islands	GGT013	KY250252
Gaidropsarus macrophthalmus	Galicia	GGR001	KY250269
Gaidropsarus macrophthalmus	Galicia	GGR002	KY250257
Gaidropsarus macrophthalmus	Galicia	GGR005	KY250281
Gaidropsarus macrophthalmus	Galicia	GGR007	KY250270
Gaidropsarus macrophthalmus	Galicia	GGR008	KY250271
Gaidropsarus macrophthalmus	Galicia	GGR009	KY250272
Gaidropsarus macrophthalmus	Galicia	GGR010	KY250273
Gaidropsarus macrophthalmus	Galicia	GGR011	KY250274
Gaidropsarus macrophthalmus	Galicia	GGR012	KY250275
Gaidropsarus macrophthalmus	Galicia	GGR013	KY250276
Gaidropsarus macrophthalmus	Galicia	GGR014	KY250277
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Gaidropsarus macrophthalmus	Galicia	GGR016	KY250279
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Gaidropsarus macrophthalmus	Andalucía	GGR034	KY250253
Gaidropsarus macrophthalmus	Andalucía	GGR035	KY250254
Gaidropsarus macrophthalmus	Bay of Biscay	GGR036	KY250255
Gaidropsarus macrophthalmus	Corsica	GGR037	KY250256
Gaidropsarus macrophthalmus	Corsica	GGR038	KY250268
Gaidropsarus macrophthalmus	Gulf of Lion	GGR039	KY250258
Gaidropsarus macrophthalmus	Scotland	GGR040	KY250259
Gaidropsarus macrophthalmus	Porcupine Sea bight	GGR041	KY250260
Gaidropsarus macrophthalmus	Porcupine Sea bight	GGR042	KY250261
Gaidropsarus macrophthalmus	Porcupine Sea bight	GGR043	KY250262
Gaidropsarus macrophthalmus	Porcupine Sea bight	GGR044	KY250263
Gaidropsarus macrophthalmus	Porcupine Sea bight	GGR045	KY250264
Gaidropsarus macrophthalmus	Porcupine Sea bight	GGR046	KY250265
Gaidropsarus macrophthalmus	Porcupine Sea bight	GGR047	KY250266
Gaidropsarus macrophthalmus	Porcupine Sea bight	GGR048	KY250267
Gaidropsarus mediterraneus	Galicia	GGD001	KY250282
Gaidropsarus mediterraneus	Galicia	GGD002	KY250285
Gaidropsarus mediterraneus	Galicia	GGD003	KY250284
Gaidropsarus mediterraneus	Galicia	GGD004	KY250283

Gaidropsarus mediterraneus	Galicia	GGD005	KY250296
Gaidropsarus mediterraneus	Galicia	GGD006	KY250295
Gaidropsarus mediterraneus	Galicia	GGD007	KY250294
Gaidropsarus mediterraneus	Galicia	GGD008	KY250293
Gaidropsarus mediterraneus	Galicia	GGD009	KY250292
Gaidropsarus mediterraneus	Galicia	GGD010	KY250291
Gaidropsarus mediterraneus	Galicia	GGD011	KY250290
Gaidropsarus mediterraneus	Galicia	GGD012	KY250289
Gaidropsarus mediterraneus	Galicia	GGD013	KY250288
Gaidropsarus mediterraneus	French Brittany	GGD014	KY250287
Gaidropsarus mediterraneus	French Brittany	GGD015	KY250286
Gaidropsarus vulgaris	Galicia	GGU001	KY250302
Gaidropsarus vulgaris	Galicia	GGU002	KY250301
Gaidropsarus vulgaris	Galicia	GGU003	KY250315
Gaidropsarus vulgaris	Galicia	GGU004	KY250300
Gaidropsarus vulgaris	Galicia	GGU005	KY250303
Gaidropsarus vulgaris	Galicia	GGU006	KY250304
Gaidropsarus vulgaris	Galicia	GGU007	KY250305
Gaidropsarus vulgaris	Galicia	GGU008	KY250306
Gaidropsarus vulgaris	Galicia	GGU009	KY250307
Gaidropsarus vulgaris	French Brittany	GGU010	KY250308
Gaidropsarus vulgaris	Galicia	GGU011	KY250309
Gaidropsarus vulgaris	Galicia	GGU012	KY250310
Gaidropsarus vulgaris	Galicia	GGU013	KY250311
Gaidropsarus vulgaris	Galicia	GGU014	KY250312
Gaidropsarus vulgaris	Galicia	GGU015	KY250313
Gaidropsarus vulgaris	Galicia	GGU016	KY250314
Gaidropsarus sp. 1	Galicia	ROL001	KY250298
Gaidropsarus sp. 1	Galicia	ROL002	KY250297
Gaidropsarus sp. 2	Bay of Biscay	GDF001	KY250299
Gaidropsarus sp. 3	Mauritania	ZDM001	

Table S2. *Gaidropsarus* query dataset (n = 22)

Taxonomic identification	Region	Database ID[1]	Barcoding assignation
Gaidropsarus argentatus	Greenland	GLF114-14	*Gaidropsarus argentatus*
Gaidropsarus argentatus	Newfoundland and Labrador	KC015386	*Gaidropsarus argentatus*
Gaidropsarus argentatus	Nunavut (Canada)	KC015387	*Gaidropsarus argentatus*
Gaidropsarus argentatus	Newfoundland and Labrador	KC015388	*Gaidropsarus argentatus*
Gaidropsarus argentatus	Gulf of St. Lawrence	KC015389	*Gaidropsarus ensis*
Gaidropsarus ensis	Greenland	GLF117-14	*Gaidropsarus ensis*
Gaidropsarus ensis	Newfoundland and Labrador	KC015390	*Gaidropsarus ensis*
Gaidropsarus ensis	Newfoundland and Labrador	KC015391	*Gaidropsarus ensis*
Gaidropsarus ensis	Newfoundland and Labrador	KC015392	*Gaidropsarus ensis*
Gaidropsarus ensis	Nunavut (Canada)	KC015393	*Gaidropsarus ensis*
Gaidropsarus ensis	Nova Scotia	KC015394	*Gaidropsarus ensis*
Gaidropsarus ensis	Bear Seamount (USA)	KF929907	*Gaidropsarus ensis*
Gaidropsarus mediterraneus	Algarve (Portugal)	JQ774626	*G. biscayensis-G. macrophthalmus*
Gaidropsarus mediterraneus	Malta	KJ709762	*G. biscayensis-G. macrophthalmus*
Gaidropsarus mediterraneus	Malta	KJ709763	*G. biscayensis-G. macrophthalmus*
Gaidropsarus mediterraneus	Malta	KJ709764	*G. biscayensis-G. macrophthalmus*
Gaidropsarus mediterraneus	Black Sea	KP136735	*G. biscayensis-G. macrophthalmus*
Gaidropsarus vulgaris	Kattegat (Sweden)	KJ128491	*Gaidropsarus vulgaris*
Gaidropsarus vulgaris	Sweden	KJ128492	*Gaidropsarus vulgaris*
Gaidropsarus vulgaris	Galicia	SFM036-13	*Gaidropsarus vulgaris*
Gaidropsarus vulgaris	Galicia	SFM037-13	*G. guttatus-G. mediterraneus*
Gaidropsarus vulgaris	Galicia	SFM038-13	*G. vulgaris*

[1]BOLD Process ID or GenBank Accession Number

Table S3. *Gaidropsarus* COI haplotype distribution (n = 52)

No. Sequences	GenBank Accession Number or BOLD process ID
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1	KY250218
1	KY250299
4	KY250179 KY250185 KY250175 KY250173
14	KY250169 KY250192 KY250190 KY250189 KY250188 KY250184 KY250183 KY250181 KY250180 KY250171 GLF114-14 KC015386 KC015387 KC015388
4	KY250191 KY250176 KY250174 KY250172
1	KY250187
1	KY250186
1	KY250182
1	KY250177
1	KY250170
1	KY250178
2	KY250239 GGA003
1	KY250238
1	KY250282
1	KY250296
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1	KY250290
1	KY250269
1	KY250274
1	KY250255
1	KY250268
1	KY250261
1	KY250262
1	KY250266
1	KY250240
12	KY250241 KY250243 KY250249 KY250252 KY250285 KY250283 KY250293 KY250292 KY250288 KY250287 KY250286 SFM037-13
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3	KY250244 KY250250 KY250284
2	KY250245 KY250248
3	KY250246 KY250291 KY250289
1	KY250247
1	KY250251
15	KY250302 KY250301 KY250300 KY250303 KY250305 KY250306 KY250307 KY250308 KY250309 KY250310 KY250311 KY250313 KY250314 SFM036-13 SFM038-13
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3	KY250304 KJ128491 KJ128492
1	KY250312
16	KY250210 KY250208 KY250203 KY250201 KY250200 KY250199 KY250198 KY250270 KY250276 KY250277 KY250278 KY250280 KY250256 KY250258 KJ709763 KJ709764
4	KY250193 KY250275 KY250263 KY250265
5	KY250209 KY250207 KY250206 KY250253 KY250254
1	KY250205
1	KY250204
9	KY250202 KY250196 KY250257 KY250272 KY250279 KY250259 KY250260 KY250264 KY250267
3	KY250197 KY250281 KP136735
1	KY250195
5	KY250194 KY250271 KY250273 JQ774626 KJ709762
1	KC015393
2	KY250298 KY250297
1	ZDM001


Gaidropsarus macrophthalmus KY250264
Gaidropsarus macrophthalmus KY250267
Gaidropsarus macrophthalmus KY250260
Gaidropsarus macrophthalmus KY250259
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Gaidropsarus biscayensis KY259196
Gaidropsarus biscayensis KY250202
Gaidropsarus biscayensis KY250194
Gaidropsarus macrophthalmus KY250271
Gaidropsarus macrophthalmus KY250273
Gaidropsarus mediterraneus JQ774626
Gaidropsarus mediterraneus KJ709762
Gaidropsarus macrophthalmus KY250266
Gaidropsarus macrophthalmus KY250255
Gaidropsarus biscayensis KY250205
Gaidropsarus biscayensis KY250193
Gaidropsarus macrophthalmus KY250275
Gaidropsarus macrophthalmus KY250263
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Gaidropsarus biscayensis KY250195
Gaidropsarus biscayensis KY250204
Gaidropsarus biscayensis KY250209
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Gaidropsarus biscayensis KY250206
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Gaidropsarus macrophthalmus KY250268
Gaidropsarus macrophthalmus KY250274
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Gaidropsarus biscayensis KY250210
Gaidropsarus biscayensis KY250208
Gaidropsarus biscayensis KY250203
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Gaidropsarus biscayensis KY250200
Gaidropsarus biscayensis KY250199
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Gaidropsarus macrophthalmus KY250261
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Gaidropsarus biscayensis KY250197
Gaidropsarus macrophthalmus KY250281
Gaidropsarus mediterraneus KP136735
Gaidropsarus granti KY250239
Gaidropsarus granti KY370633
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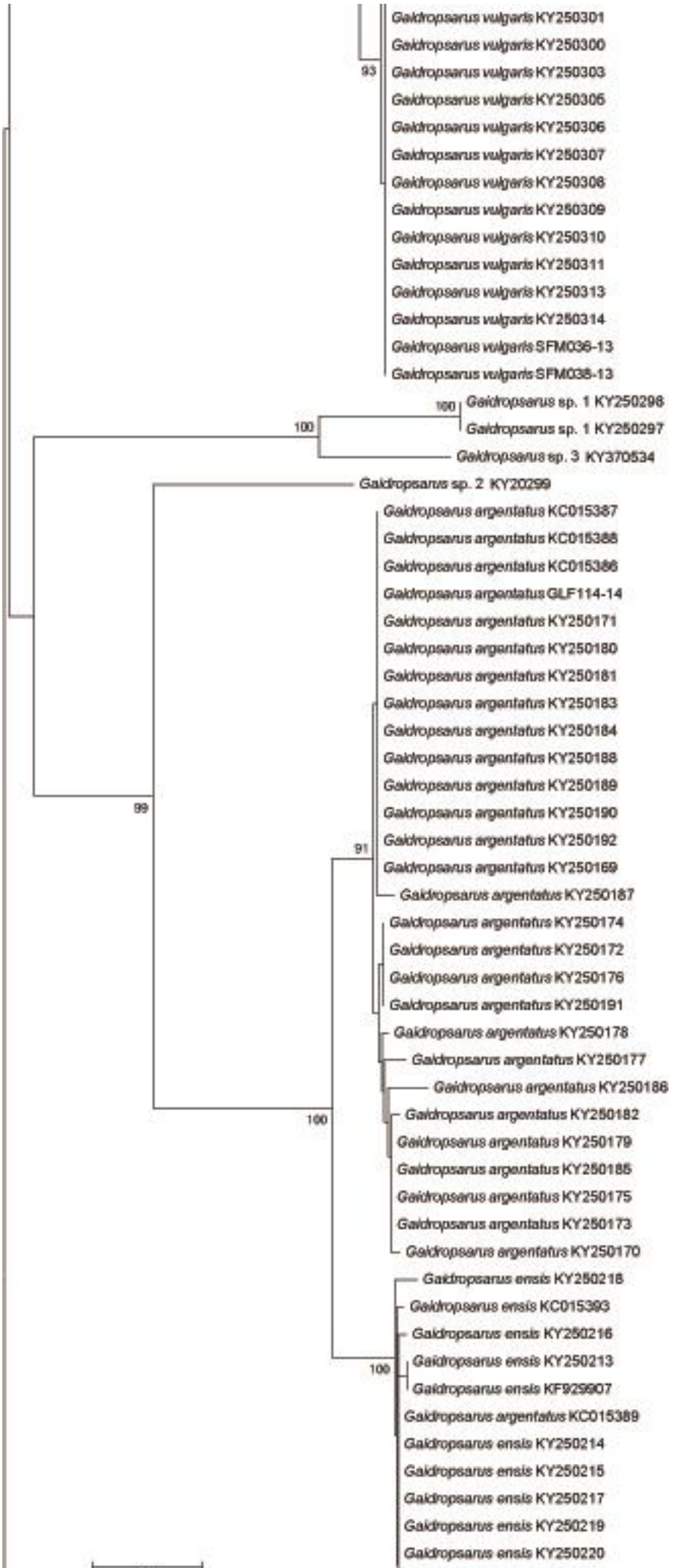
98
100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Gaidropsarus vulgaris KY250314
Gaidropsarus vulgaris SFM036-13
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Gaidropsarus sp. 2 KY20299
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Gaidropsarus argentatus KC015388
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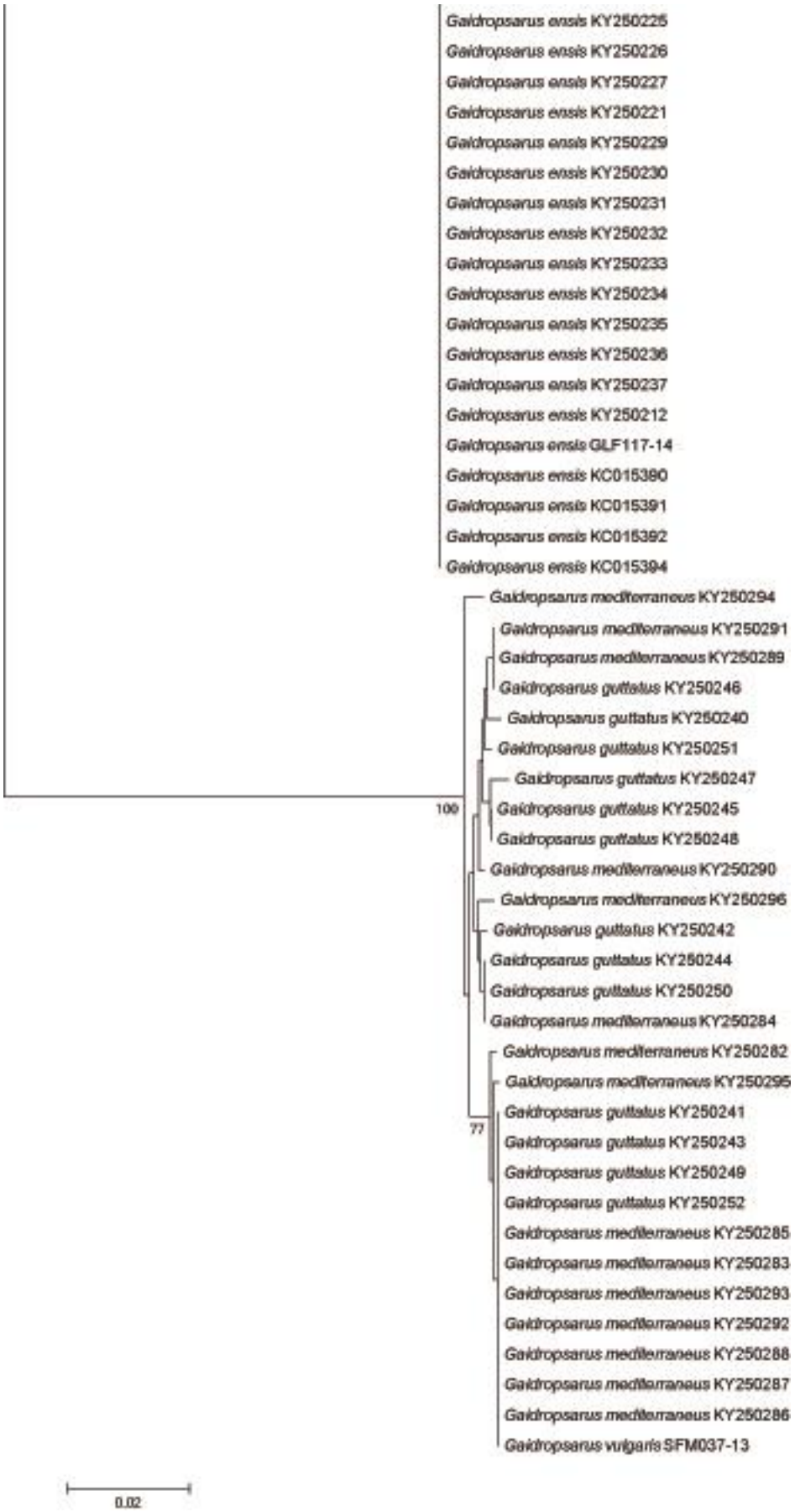
Gaidropsarus ensis KY250220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Gaidropsarus ensis KY250237
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