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It makes a difference who you are: first record of *Dasyatis tortonesei* Capapé, 1975 along Sardinian coasts and taxonomic uncertainties within stingrays

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ABSTRACT
Despite several records of *Dasyatis tortonesei* Capapé, 1975 in the Mediterranean Sea, its distribution and abundance have been questioned due to the cryptic nature of the Tortonese's stingray and the frequent misidentification with the common stingray *Dasyatis pastinaca* (Linnaeus, 1758). Through morphological and molecular analyses, the two species had been confirmed in previous studies, but uncertainties remain about their distribution and presence, and the effectiveness of morphological and molecular discrimination between these two stingrays. Additionally, *D. tortonesei* suffers from limited availability of biological information, in part due to the abovementioned taxonomic ambiguity, hampering adequate conservation actions. In fact, *D. tortonesei* is listed as Data Deficient on the International Union for Conservation of Nature (IUCN) Red List, while *D. pastinaca* is classified as Vulnerable. The catching of an "unusual" stingray along the Sardinian coast led us to hypothesize that it could be a *D. tortonesei* individual. Since the correct identification of specimens is necessary to properly assess the impact of fisheries, and stingrays share many morphological similarities, molecular identification of this specimen was conducted using mtDNA markers. Additional specimens of stingrays were sampled in the same area. New and public sequences of COI and NADH2 mitochondrial genes were analysed. Sequence data confirmed the occurrence of *D. tortonesei* in the investigated area, highlighting the frequent misidentification between this species and closely related species in the field, and underscoring the need for updated and reliable morphological identification keys. To evaluate whether the misidentification issue involves other Mediterranean stingrays, an extensive molecular analysis, including multiple species, was performed. The application of several species-delimitation methods revealed widespread taxonomic uncertainties across the five genera of the Mediterranean Dasyatidae. These results point out unresolved systematic issues within the family and emphasize the urgent need for further integrative taxonomic studies and a comprehensive revision of the taxon, essential to support effective conservation strategies.

HIGHLIGHTS

- First six confirmed records of *Dasyatis tortonesei* in Sardinian waters (Western Mediterranean Sea)
- High misidentification rate between *Dasyatis pastinaca* and *D. tortonesei*
- Integrative taxonomic revision needed for Mediterranean stingrays

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Introduction

Anthropogenic impacts such as fishing activities and habitat degradation are producing negative effects on several taxonomic groups found in the Mediterranean Sea, including cartilaginous fish species (Coll et al. 2010; Micheli et al. 2013; Dulvy et al. 2021; Walls & Dulvy 2021; Albonetti et al. 2023), with their abundance in continuous decline (Stein et al. 2018; Dulvy et al. 2021). This is especially true for Mediterranean elasmobranchs, which frequently face a greater risk of extinction than those found in other maritime regions (Dulvy

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et al. 2021; Walls & Dulvy 2021; Albonetti et al. 2023). Given the spatial overlap of fisheries with species' ranges, sharks and rays are commonly caught in fishing gear such as nets, longlines, and bottom trawls (Follesa et al. 2019; Carpentieri et al. 2021; Scacco et al. 2023, 2023). However, due to low market demand and economic value, they are generally considered bycatch (Vella et al. 2017; Carpentieri et al. 2021; Vella & Vella 2021). Additionally, elasmobranchs are rarely reported in official fishery reports and are often grouped into broad, generic categories; for this reason, some species could be affected by higher risk levels than officially assessed (Cashion et al. 2019; Jorgensen et al. 2019, 2022; Cortés et al. 2023). This may be caused by heavy pressure on particular and delicate species' life stages, loss of fitness and/or competitive capability, and incorrect estimation of species abundance and distribution (Cashion et al. 2019; Villagra et al. 2022; Maioli et al. 2023; Bellodi et al. 2024). Furthermore, many species can be confused through the presence of similar phenotypic traits that can complicate their identification and consequently their assessment (Cariani et al. 2017; Daly-Engel et al. 2018, 2019; van der Bank 2019; Ferrari et al. 2021, 2023; Chatzispyrou & Koutsikopoulos 2023; Melis et al. 2023; Ehemann et al. 2024; Weigmann et al. 2024). In the Mediterranean Sea, this issue is particularly evident for batoids, which – despite being common components of fisheries bycatch – have received considerably less scientific and conservation attention than sharks, partly due to their lower public and research visibility (Jorgensen et al. 2022; Davidson et al. 2022). The overlapping of all these factors greatly limits the ability to assess the distribution, abundance, and fishing impact on these species and their populations, as well as to identify distribution patterns and seasonal movements (Cashion et al. 2019; Mariani et al. 2021).

As an example, two morphologically similar stingrays of the family Dasyatidae are frequently misidentified: *Dasyatis tortonesei* Capapé, 1975 and *Dasyatis pastinaca* (Linnaeus, 1758) (Last et al. 2016; Coelho 2017; Ebert & Dando 2020; Vella & Vella 2021; Barone et al. 2022). For many years, *D. tortonesei*'s taxonomic status has been questioned, and the species has often been treated as a synonym of *D. pastinaca* (Ebert & Stehmann 2013; Serena et al. 2020; Barone et al. 2022). This long-standing uncertainty has hindered the validation of its existence and geographical distribution, limiting the availability of species-level data (Barone et al. 2022). Although morphological and molecular analyses support the distinctiveness of the two species (Saadaoui et al. 2016; Vella & Vella 2021), uncertainties persist regarding their distribution and the reliability of diagnostic characters (Barone et al. 2022; Giagkazoglou et al. 2022), leading to inaccurate assessments.

The common stingray *D. pastinaca* is found along the northern Atlantic coast, including the Mediterranean Sea, while the Tortonese's stingray *D. tortonesei* has only been reported in the Mediterranean Sea (Ebert & Dando 2020). Current records of *D. tortonesei* are limited to the Sea of Marmara (Yıldız et al. 2016) and the central Mediterranean Sea, including Tunisian and Maltese waters (Capape 1978; Capapé et al. 2012; Vella et al. 2017; Vella & Vella 2021). These two medium-sized stingrays are frequently captured by small-scale local artisan fishermen and are often grouped under generic terms in the fish market (e.g. "rays" or "stingrays") or easily misidentified during field activity (Bradai 2012; Ebert & Stehmann 2013; Yıldız et al. 2016; Vella et al. 2017; Vella & Vella 2021; Barone et al. 2022). Although new records of *D. tortonesei* have been reported in recent years, improving our knowledge and defining its geographical range at a finer scale (Yıldız et al. 2016; Ebert & Dando 2020; Serena et al. 2020; Vella & Vella 2021; Saidi et al. 2023), much remains unknown about its distribution, biology, and ecology. Consequently, there are insufficient biological data on *D. tortonesei*, which makes it difficult to take adequate conservation measures. In fact, while *D. pastinaca* is classified as Vulnerable on the global, European, and Mediterranean lists due to a declining population trend caused by fishing, tourism, and recreational activities (Serena et al. 2015, 2016; Jabado et al. 2021), *D. tortonesei* is actually listed as Data Deficient on the International Union for Conservation of Nature (IUCN) Red List at the global level (Jabado & Derrick 2021).

A very likely misidentification rate combined with a dearth of records and specialized studies has undoubtedly introduced bias, resulting in a plausible underestimation of *D. tortonesei's* occurrence and consequently population structure, abundance, and distribution.

With this in mind, this work aims to report the first record of *D. tortonesei* along the Sardinian coasts (Western Mediterranean Sea) as well as to provide new information using molecular taxonomic tools that can assist future studies in the accurate identification of the Tortonese's stingray. Moreover, this work aims to investigate the species belonging to the five genera of Dasyatidae reported to be present in the Mediterranean Sea to address whether similar taxonomic uncertainties and identification issues exist. Actually, recent studies underlined that misidentifications and morphologically cryptic species could be very common in morphologically conservative groups such as sharks, rays and their relatives (Naylor et al. 2012; Last et al. 2016; Weigmann 2016; Coelho 2017; Borsa 2017; Bineesh et al. 2017; van der Bank 2019; Ariza et al. 2022; Weigmann et al. 2024; Di Crescenzo et al. 2024), making it difficult to distinguish between both known and unknown species. After downloading public sequences of multiple species of Dasyatidae and combining them with newly produced data, we found evidence of cryptic species, widespread taxonomic uncertainties, and phylogenetic issues to be addressed in future studies.

Material and methods

Putative specimens of *D. pastinaca* (*n* = 23) and *D. tortonesei* (*n* = 1) were collected during the MEDITS (MEDiterrranean International Trawl Survey) scientific survey (Spedicato et al. 2019) conducted in the General Fisheries Commission for the Mediterranean of Food and Agriculture Organization of the United Nations (FAO-GFCM) Geographic Sub-Area (GSA) 11 – Sardinia during the 2023 campaign (Figures 1 and 2; Table SM1) and through opportunistic bottom trawl samplings. Morphological identification of specimens was conducted by integrating information retrieved from Saadaoui et al. (2016), Ebert and Dando (2020) and Barone et al. (2022). A tissue sample (muscle or fin clip) was collected for each individual and preserved in 96% ethanol.

According to Giagkazoglou et al. (2022), molecular identification was conducted using a double assay. In particular, COI and NADH2 sequences were used in this investigation. In order to increase the resolution power of molecular analysis, we also processed samples for other stingray species that were collected in

Figure 1. Dorsal and ventral views (left and right, respectively) of *D. pastinaca* and *D. tortonesei*.

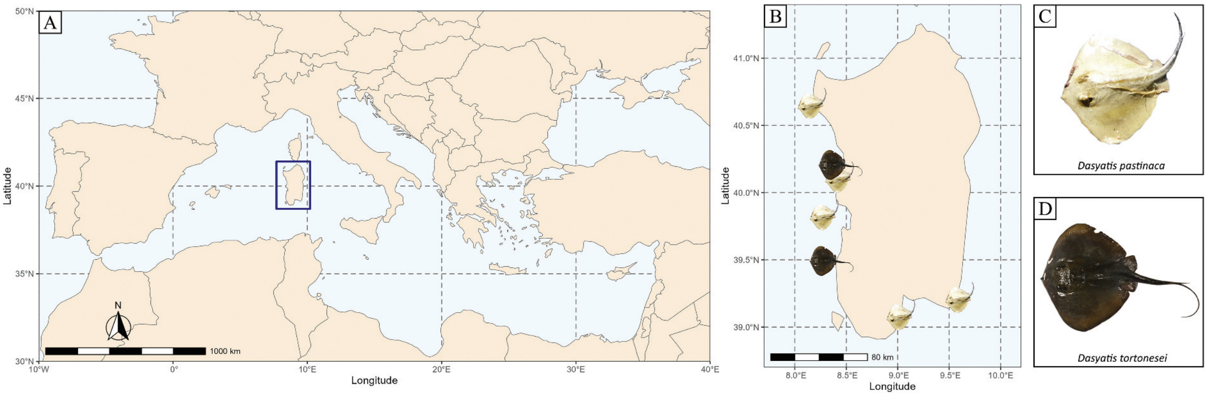

Figure 2. Map of the Mediterranean highlighting the study area (A) and a close-up of Sardinia with the sampling points (B) where *D. pastinaca* (C) and *D. tortonesei* (D) specimens (confirmed by molecular tools) were collected.

Sardinia during sampling activities: *Pteroplatytrygon violacea* (Bonaparte, 1832) (*n* = 4), *Bathytoshia lata* (Garman, 1880) (*n* = 5); while *Aetomylaeus bovinus* (Geoffroy Saint-Hilaire, 1817) (*n* = 6) was used as the outgroup (Table SM1). The species names used in this study followed the nomenclature proposed by Saadaoui et al. (2016), Ebert and Dando (2020), and Barone et al. (2022) and are in accordance with the World Register of Marine Species (WoRMS Editorial Board 2025).

Total genomic DNA (gDNA) was extracted following the PureLink Genomic DNA Mini Kit (Invitrogen). Polymerase chain reactions (PCRs) were performed in a total volume of 25 µL containing 1x PCR buffer (MgCl and dNTPs included), 1.0 pmol of each primer and 1.0 U of WonderTaq Hot Start DNA polymerase (EuroClone) using a Mastercycler EP Gradient S Eppendorf (Biometra). A fragment of the COI mitochondrial gene was obtained from each specimen by PCR using the FishF2 and FishR1 primers (Ward et al. 2005). PCR reactions were performed with an initial denaturation of 3 min at 95°C, followed by 35 cycles of 30 s at 95°C, 30 s at 54°C and 60 s at 72°C and a final extension step for 5 min at 72°C. Similarly, a fragment of the NADH2 mitochondrial gene was amplified using the ND2-MetF and ND2-TrpR primers (Vella et al. 2017). PCR conditions consisted of an initial denaturation of 3 min at 95°C, followed by 35 cycles of 30 s at 95°C, 45 s at 56°C and 45 s at 72°C and a final extension step for 10 min at 72°C. All the amplicons were sequenced by the external provider Macrogen Europe (Milan, Italy).

The new COI and NADH2 sequences obtained were imported and aligned with the CLUSTAL W algorithm (Thompson et al. 1994) implemented in MEGA 12 (Kumar et al. 2024). COI and NADH2 available sequences of the five stingray genera inhabiting the Mediterranean Sea (*Bathytoshia*, *Dasyatis*, *Himantura*, *Pteroplatytrygon* and *Taeniurops*) (Ebert & Dando 2020; Serena et al. 2020; Barone et al. 2022) were retrieved from GenBank (National Center for Biotechnology Information; NCBI) (Federhen 2012; Sayers et al. 2022) and Barcode of Life Data Systems (BOLD) databases (Ratnasingham et al. 2024) to compare newly produced and already available sequences (SM1). The script-based search of available sequences was performed following (Melis et al. 2023). A total of 1035 COI and 134 NADH2 public sequences were retrieved and downloaded to be used in further analyses.

New and already available sequences were collapsed into haplotypes using DNASP v. 6 (Rozas et al. 2017).

Species partitions (Miralles et al. 2022, 2024) were performed for the Mediterranean stingray species clusters using the TCS method (Clement et al. 2002) implemented in the software Hapsolutely v. 0.2.2 (Vences et al. 2024). Haplotype networks were built separately for each genus except for *Pteroplatytrygon* and *Taeniurops*, which were analysed together.

Based on recent studies, the genetic-based taxon identification was grounded in multiple species delimitation methods (Karabanov et al. 2023). COI and NADH2 sequences were analysed using four tree-based approaches: (i) the Poisson Tree Process (PTP) (Zhang et al. 2013), (ii) the Multi-rate Poisson Tree Processes (mPTP) (Kapli et al. 2017), (iii) the Bayesian Poisson Tree Process (bPTP) (Zhang et al. 2013), and (iv) the Bayesian tree reconstruction based on the Yule speciation process (YSP) (Gernhard 2008), performed with Beast v. 1.10.4 (Suchard et al. 2018).

PTP, mPTP, and bPTP were carried out using Maximum Likelihood (ML) trees, which were obtained in the PhyML v. 3.0 web server (http://www.atgc-montpellier.fr/phyml) (accessed on 25 August 2025) (Guindon et al. 2010) by applying default settings. Automatic selection for the best substitution model was determined with the Akaike information criterion (AIC) of the Smart Model Selection (SMS) (Lefort et al. 2017) already implemented into PhyML v. 3.0 as an online tool.

PTP and mPTP analyses were performed on online software (http://mptp.h-its.org) (accessed on 25 August 2025) using default settings (*p*- value set to 0.001 for PTP). Similarly, the bPTP analysis was conducted on a web server (http://species.h-its.org/ptp) (accessed on 25 August 2025) using default settings. The YSP analyses were carried out using the GTR+G+I and TN93+G+I substitution models (according to SMS outputs) for NADH2 and COI, respectively, strict clock type, running 50,000,000 MCMC generations sampled every 1000 generations with a 20% burn-in. Log files were analysed with Tracer v. 1.7.2 (Rambaut et al. 2018). The YSP Bayesian trees obtained were summarized in a single Maximum Clade credibility tree using TreeAnnotator included in Beast v. 1.10.4 (Suchard et al. 2018).

Sequences were also analysed using distance-based approaches by performing Assemble Species by Automatic Partitioning (ASAP) (Puillandre et al. 2021). The ASAP analysis was carried out using the ASAP web server (https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html) (accessed on 25 August 2025), choosing the simple distance (p-distance) to calculate the pairwise distance. Additionally, for the COI sequences, molecular operational taxonomic nits (MOTUs) were also delimited using the Barcode Index Numbers (BINs) as defined in BOLD (Ratnasingham et al. 2024).

As the different methods can lead to conflicting results, we considered a reliable result the consensus shared by the majority of the methods applied. Newly produced and public COI and NADH2 sequences of *A. bovinus* were employed as outgroup for all analyses previously described (Table SM1).

Results

DNA was successfully extracted, amplified and sequenced for 35 and 39 individuals for COI and NADH2 mtDNA markers, respectively (Table SM1). The newly produced COI sequences count 626 bp for *D. pastinaca* and *D. tortonesei*, while the length of the sequences was 602 bp for *A. bovinus, B. lata*, and *P. violacea* specimens. Similarly, we obtained a newly produced NADH2 sequence dataset of 936 bp for all five species analysed. A total of 12 and 20 haplotypes were retrieved for COI and NADH2, respectively (Table SM1).

The comparison of newly produced sequences immediately revealed the occurrence of misidentifications. In particular, five samples morphologically identified as *D. pastinaca* (R_Dp334, R_Dp335, R_Dp336, R_Dp338, R_Dp339) shared COI haplotypes with the single specimen morphologically identified as *D. tortonesei* (R_Dt01; Table SM1). Additionally, a sample morphologically identified as *B. lata* (R_Bc04) shared the COI haplotype with 13 *D. pastinaca* specimens (Table SM1). Similar results were obtained examining the NADH2 sequences. These preliminary outputs suggest that the number of Sardinian Tortonese's stingrays amounts to six individuals.

To address whether similar misidentifications exist involving other Mediterranean stingray species, newly produced and public sequences were merged: the two final datasets counted 1070 COI sequences (276 haplotypes; 544 bp) and 173 NADH2 sequences (105 haplotypes; 891 bp) (Table SM1).

Upon examining the COI and NADH2 haplotype networks constructed for every genus, we discovered that several nominal species shared haplotypes, suggesting the occurrence of several misidentification/mislabelling cases. Concerning the genus *Dasyatis*, we observed that *D. pastinaca* was easily misidentified with the congeneric species *D. tortonesei* as well as with *Dasyatis marmorata* (Steindachner, 1892) (Figure 3). On the contrary, *Dasyatis chrysonota* (Smith, 1828) did not share haplotypes with any species (Figure 3). Additionally, divergent haplotypes attributed to *D. pastinaca* and *D. marmorata* were visible in the COI network (Figure 3). In the genus *Bathytoshia*, we observed several cases of (i) haplotype sharing between species, (ii) presence of divergent haplotypes within species, and (iii) occurrence of possible misidentification/mislabelling errors between the two species *Bathytoshia centroura* (Mitchill, 1815) and *B. lata* in both datasets (Figure 4). High taxonomic uncertainty and misidentification rates were found in the genus *Himantura*. Along with *Himantura leoparda* Manjaji-Matsumoto & Last, 2008 and *Himantura uarnak* (Gmelin, 1789), our analyses revealed that at least two additional possible cryptic species could be present (Figure 5). Lastly, we observed divergent haplotypes both in *P. violacea* and *Taeniurops grabatus* (Geoffroy Saint-Hilaire, 1817) in the COI dataset, while no criticalities were found in inspecting the NADH2 haplotypes network (Figure 6).

Tree-based and distance-based species delimitation approaches were used on both datasets. The results indicated the possible occurrence of different numbers of MOTUs, ranging from 54 to 65 and from 32 to 40 in COI and NADH2, respectively (Figures 7 and 8; Table SM1). Applying the consensus criterion, we identified 59 and 39 MOTUs in the COI and NADH2 datasets, respectively (Figures 7 and 8; Table SM1). It is important to underline that 26 and 9 MOTUs (for COI and NADH2, respectively) did not correspond to a known species, suggesting that many cryptic species could occur in the family Dasyatidae.

The main outcomes of the species delimitation analyses are summarized in the Supplementary materials – Table SM2 and Table SM3 for COI and NADH2, respectively – while the full details and geographical origins of sequences (where available) are reported in Table SM1.

Our results confirm that *D. tortonesei* and *D. pastinaca* are clearly differentiated by both markers used. Moreover, *D. pastinaca* is quite different from the other congeneric species currently placed in the genus *Dasyatis* (orange label), with sequences deposited as *Dasyatis brevis* (Garman, 1880) clustering together with *Hypanus say* (Lesueur, 1817) (dark blue label), the single representative species of this genus (Figures 7 and 8).

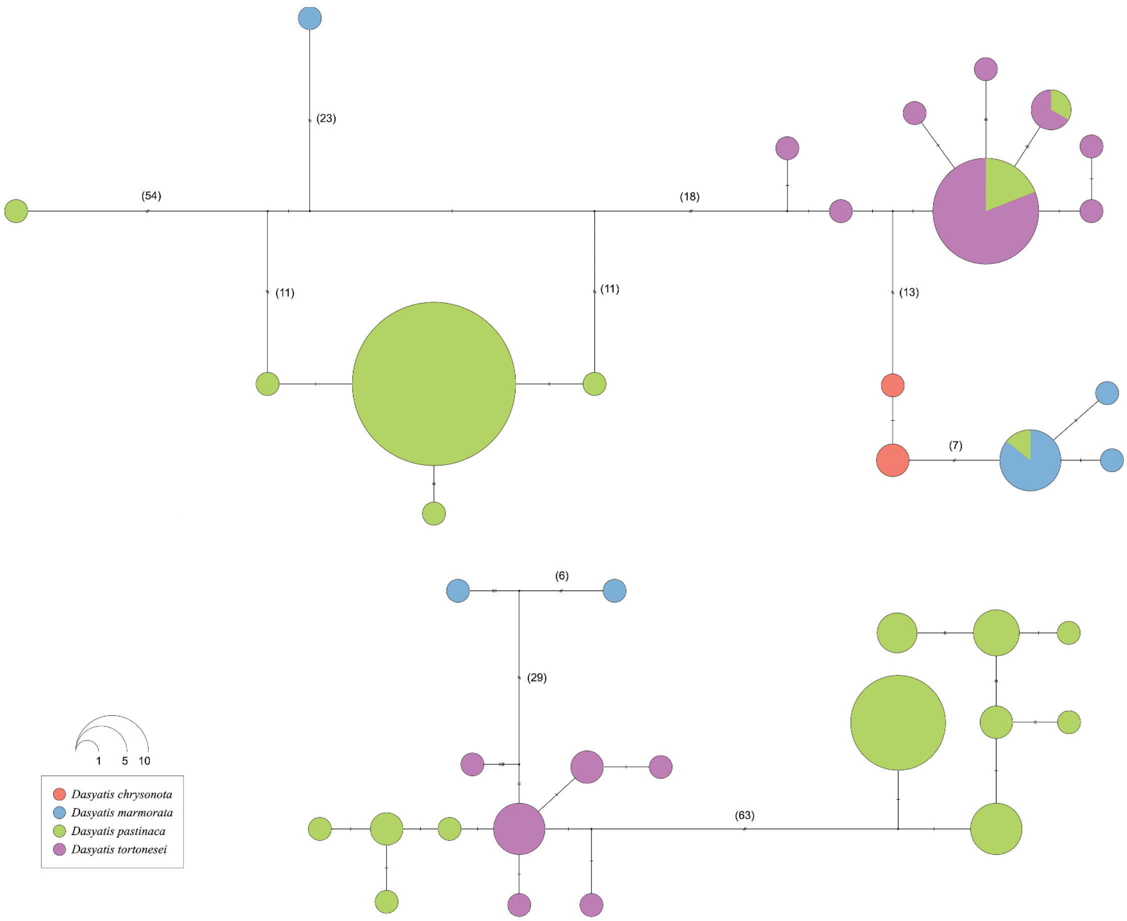

Figure 3. *Dasyatis* TCS haplotype network of COI (top) and NADH2 (bottom). Black dots represent unsampled haplotypes. The numbers in parentheses indicate the number of substitutions separating the two haplotypes.

Our delimitation analyses suggest that *B. lata* and *B. centroura* are a single species. Additionally, we observed that some COI sequences deposited as *B. lata* clustered in two MOTUs (MOTU AA and MOTU X) separated from the nominal species group but close to *Brevitrygon imbricata* (Bloch & Schneider, 1801).

A great deal of confusion was observed within the retrieved *Himantura* spp. sequences, with large numbers of misidentified/mislabelled records (Figures 7 and 8, Table SM1). A unique sequence from a Mediterranean specimen was retrieved, clustering with other *H. uarnak* sequences (Table SM1). Furthermore, many sequences deposited as *Himantura* spp. and/or *Dasyatis* spp. were found to belong to the genera *Maculabatis*, *Brevitrygon, Pateobatis*, *Hypanus*, *Megatrygon*, *Styracura*, *Urogymnus, Fontitrygon*, and *Hemitrygon* (Tables SM1, SM2, SM3).

Lastly, even though *A. bovinus* was chosen as a "simple" non-problematic outgroup, we observed that this species was divided into two MOTUs in the NADH2 analyses (*A. bovinus* and MOTU AP; Figure 8).

With both datasets, we found discrepancies in the current accepted taxonomy. In fact, phylogenetic reconstructions highlighted the lack of monophyly in the genera *Dasyatis*, *Himantura*, *Pateobatis*, and *Urogymnus* (Figures 7 and 8). Additionally, relationship between *Pteroplatytrygon* and *Bathytoshia* is controversial in the two datasets (Figures 7 and 8).

Discussion

The present study primarily aimed to confirm the occurrence of *D. tortonesei* in the Sardinian seas by applying a molecular taxonomical approach. Molecular analyses were also extended to the five genera of Dasyatidae (*Bathytoshia*, *Dasyatis*, *Himantura*, *Pteroplatytrygon* and *Taeniurops*) inhabiting the Mediterranean Sea. To reach this goal, all the available online COI and NADH2 sequences for the investigated species were

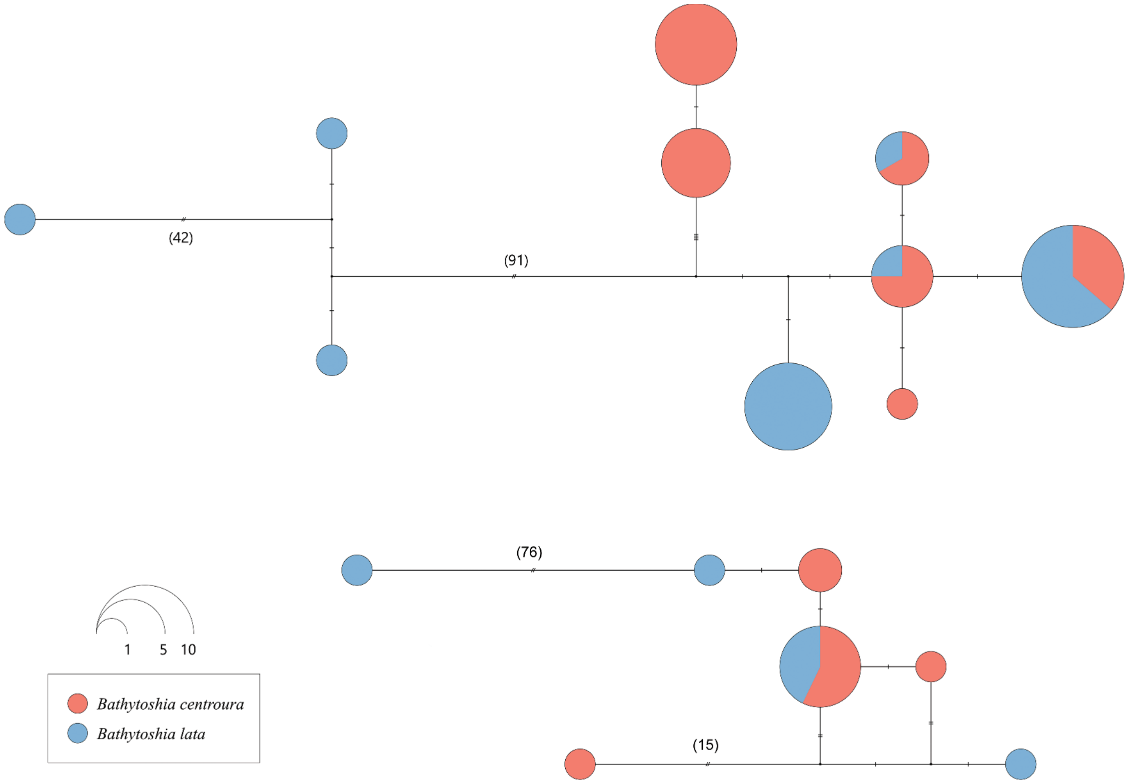

Figure 4. *Bathytoshia* TCS haplotype network of COI (top) and NADH2 (bottom). Black dots represent unsampled haplotypes. The numbers in parentheses indicate the number of substitutions separating the two haplotypes.

downloaded and analysed, aiming to delineate the occurrence of possible misidentified, undescribed and cryptic species.

Taking advantage of the recent reorganization of the family Dasyatidae, where many species were reassigned to extant, new, or resurrected genera (Last et al. 2016; Coelho 2017), we investigated the phylogenetic relationships among these species, looking for further possible revision needs for this peculiar and understudied taxonomic group.

Based on our in-field morphological identification and molecular results, the "unusual" stingray specimen R_Dt01 was finally identified as *D. tortonesei* (Table SM1). This individual was recognized based on snout and head shape differences described by Saadaoui et al. (2016). However, the results of the genetic analysis showed that five specimens initially recognized as *D. pastinaca* using the widely accepted identification keys (Ebert & Dando 2020; Barone et al. 2022) were actually *D. tortonesei*. Therefore, our data confirmed the morphological misidentification of five *D. pastinaca* samples analysed during this study, increasing the number of *D. tortonesei* caught in the Sardinian area from one to six. Furthermore, according to our results derived from morphological observation combined with concurrent molecular outputs, in Ebert and Dando (2020) drawings of *D. pastinaca* and *D. tortonesei* are incorrectly reported and ought to be switched. The converging of morphological features has made it hard to identify and use resolutive recognition characters, boosting episodes of human misidentifications involving these two species, similarly to other Mediterranean stingray species (Capapé et al. 2012; Ebert & Stehmann 2013; Vella et al. 2017; Cariani et al. 2017; Vella & Vella 2021; Kousteni et al. 2021; Barone et al. 2022; Giagkazoglou et al. 2022; Chatzispyrou & Koutsikopoulos 2023; Saidi et al. 2023) According to our findings, the morphological identification of specimens conducted following the key identification guides nowadays used may not be conclusive, and, for this reason, more resolutive and easy-to-use traits should be identified in order to facilitate in-field identification and, consequently, improve the knowledge about these poorly studied species.

Misidentification records are known to be common for stingrays: they are easily confused during in-field surveys and by fishermen due to the absence of reliable morphologically distinctive traits (Capapé et al. 2012; Ebert & Stehmann 2013; Vella et al. 2017; Cariani et al. 2017; Vella & Vella 2021; Kousteni et al. 2021; Barone et

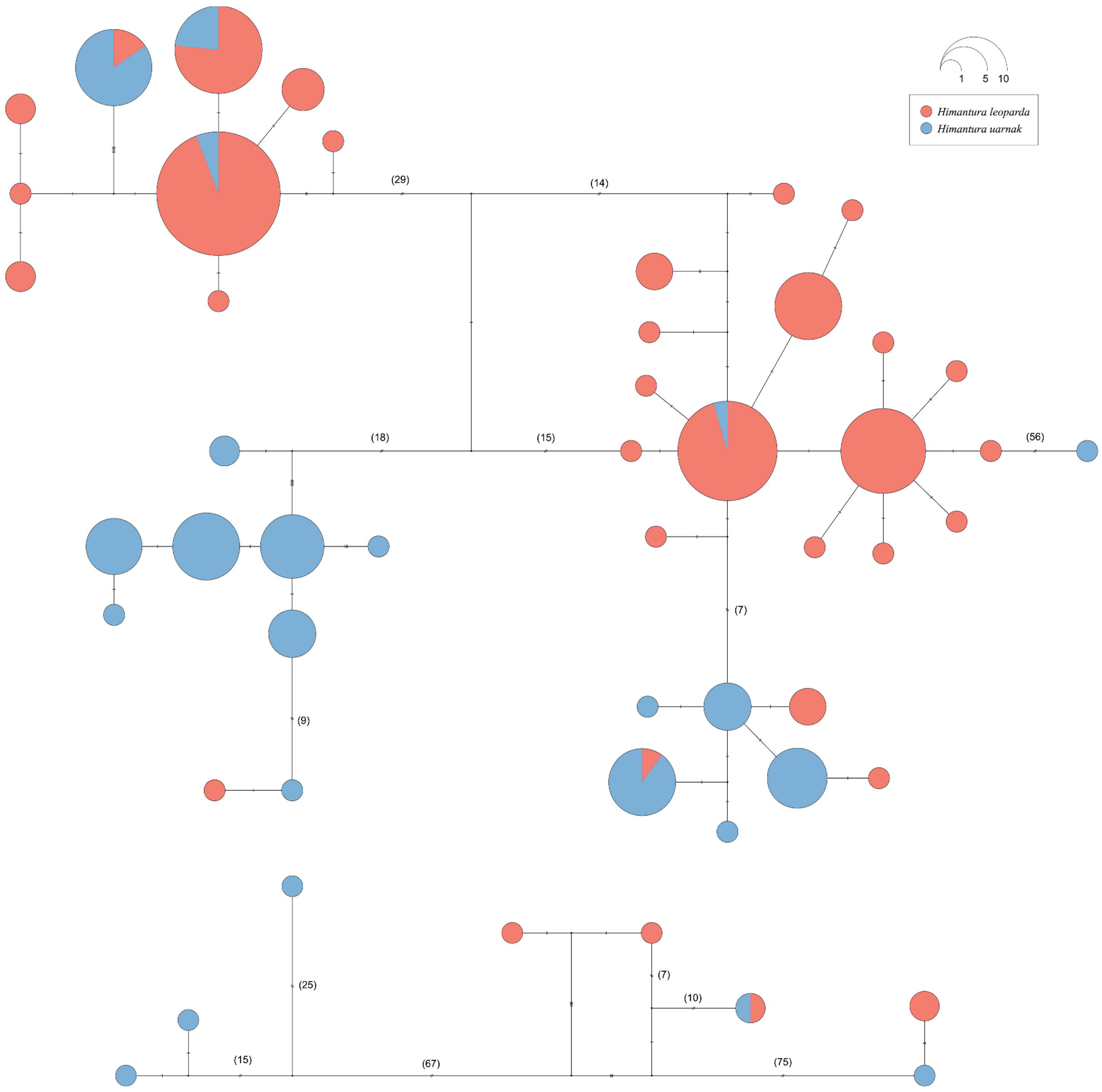

Figure 5. *Himantura* TCS haplotype network of COI (top) and NADH2 (bottom). Black dots represent unsampled haplotypes. The numbers in parentheses indicate the number of substitutions separating the two haplotypes.

al. 2022; Giagkazoglou et al. 2022; Chatzispyrou & Koutsikopoulos 2023; Saidi et al. 2023). We found evidence for misidentification involving species that are easily distinguishable morphologically, such as *D. marmorata* and *T. grabatus* (Tables SM1 and SM2). Several misidentifications occurred (*D. pastinaca* and *D. tortonesei*; *D. pastinaca* and *D. marmorata*), even between genera (*Dasyatis* and *Bathytoshia*; *Dasyatis* and *Taeniurops*). The divergent *D. marmorata* haplotype (Figure 3) was found to be *T. grabatus*, while the divergent *T. grabatus* haplotype (Figure 6) was *D. marmorata*, resulting in a reciprocal misidentification event (further details in Tables SM1 and SM2).

Stingrays typically exhibit a large number of conservative morphological traits; therefore, it is difficult to correctly classify each individual into the appropriate taxonomic category; this is particularly true for juveniles. In this context, an additional but relevant misidentification found during this study involved a juvenile morphologically identified as *B. lata* (R_Bc04) but genetically found to be *D. pastinaca*.

Concerning the individuals sequenced during this study, we observed that our *B. lata* specimens (R_Bc04 excluded) shared their haplotypes with sequences deposited in public repositories as both *B. lata* and *B. centroura* (Table SM1).

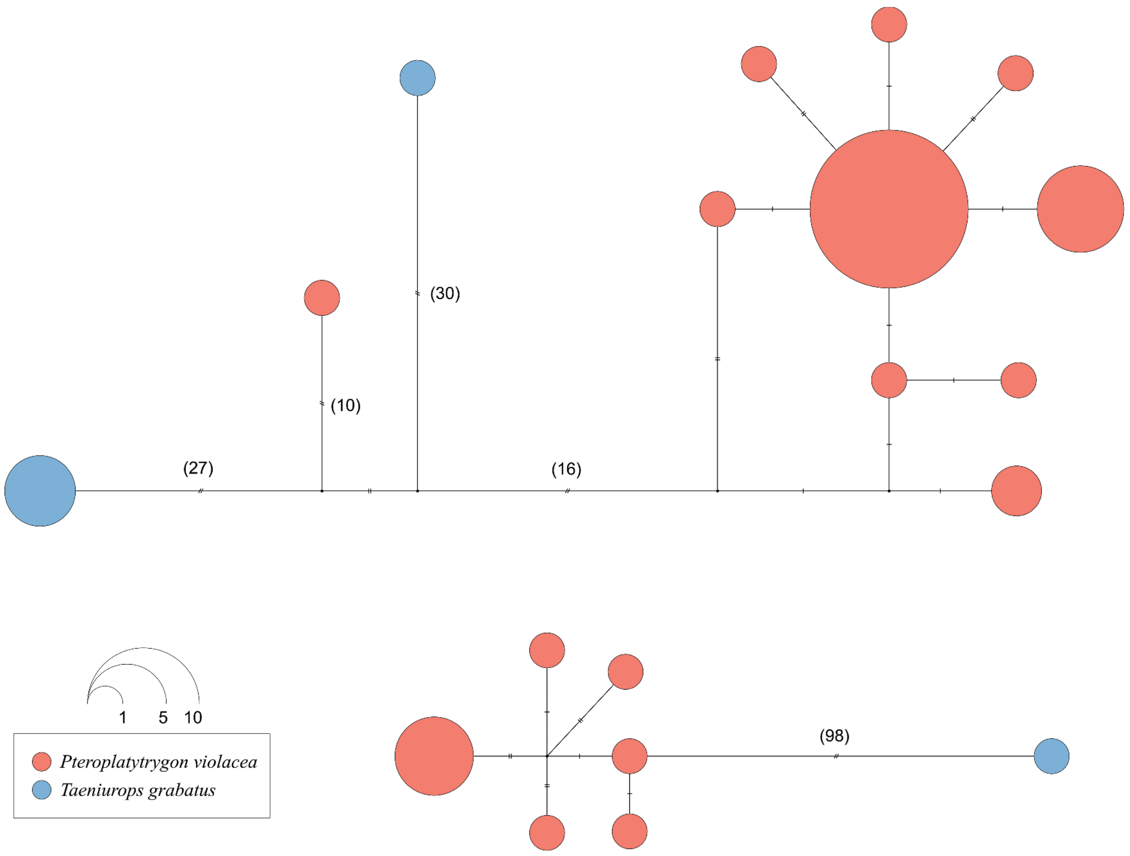

Figure 6. *Pteroplatytrygon* and *Taeniurops* TCS haplotype network of COI (top) and NADH2 (bottom). Black dots represent unsampled haplotypes. The numbers in parentheses indicate the number of substitutions separating the two haplotypes.

According to the results obtained from the species delimitation analyses, all the sequences deposited as *B. lata* and *B. centroura* from the Mediterranean Sea, the Western Atlantic Ocean, and the Indian Ocean (up to Indonesia) belong to a single species that should be named *B. centroura*, following the species denomination found in the oldest literature (Garman 1913; Ebert & Stehmann 2013; Weigmann 2016; Carpenter & De Angelis 2016), contrary to the proposal by Last et al. (2016) and Coelho (2017) to recognize two distinct species, reserving the name *B. centroura* exclusively for the Western Atlantic populations and extending the distribution of *B. lata* to include the eastern Atlantic, Indian Ocean, and Pacific. Unfortunately, further detailed comparisons were not possible since most of the sequences used by Last et al. (2016) and Coelho (2017) were not available in public repositories, nor is the (unpublished) data used to claim the occurrence of *B. lata* in the Indo-Pacific and Eastern Atlantic (Mediterranean included). Additional samples and future studies will be necessary to unravel this issue.

More examples of mislabellings/misidentifications were also found considering other taxa (genera *Brevitrygon*, *Maculabatis*, *Pateobatis*, and *Urogymnus*) the *Himantura* sequences, involving at least five congeneric species (*H. leoparda*, *H. uarnak, Himantura australis* Last, White & Naylor, 2016, and *Himantura undulata* (Bleeker, 1852), *Himantura tutul* Borsa, Durand, Shen, Alyza, Solihin & Berrebi, 2013), as well as other taxa (genera *Brevitrygon*, *Maculabatis*, *Pateobatis*, and *Urogymnus*).

Of particular interest is the current state of *H. tutul*, which is considered a synonym of *H. uarnak* according to *Eschmeyer's Catalog of Fishes* (Fricke et al. 2025) but not in the World Register of Marine Species (WoRMS Editorial Board 2025); however, the taxonomic uncertainty remains (Weigmann 2016; Borsa 2017; WoRMS Editorial Board 2025; Fricke et al. 2025). Recently, Kumar et al. (2020) recorded the species in Indian coastal waters, confirming its taxonomic distinction through molecular and species delimitation analyses, supporting the findings obtained during this work (Figure 8 and Table SM1). Future studies concerning the application of multiple and integrative approaches will surely help to unravel this taxonomic uncertainty.

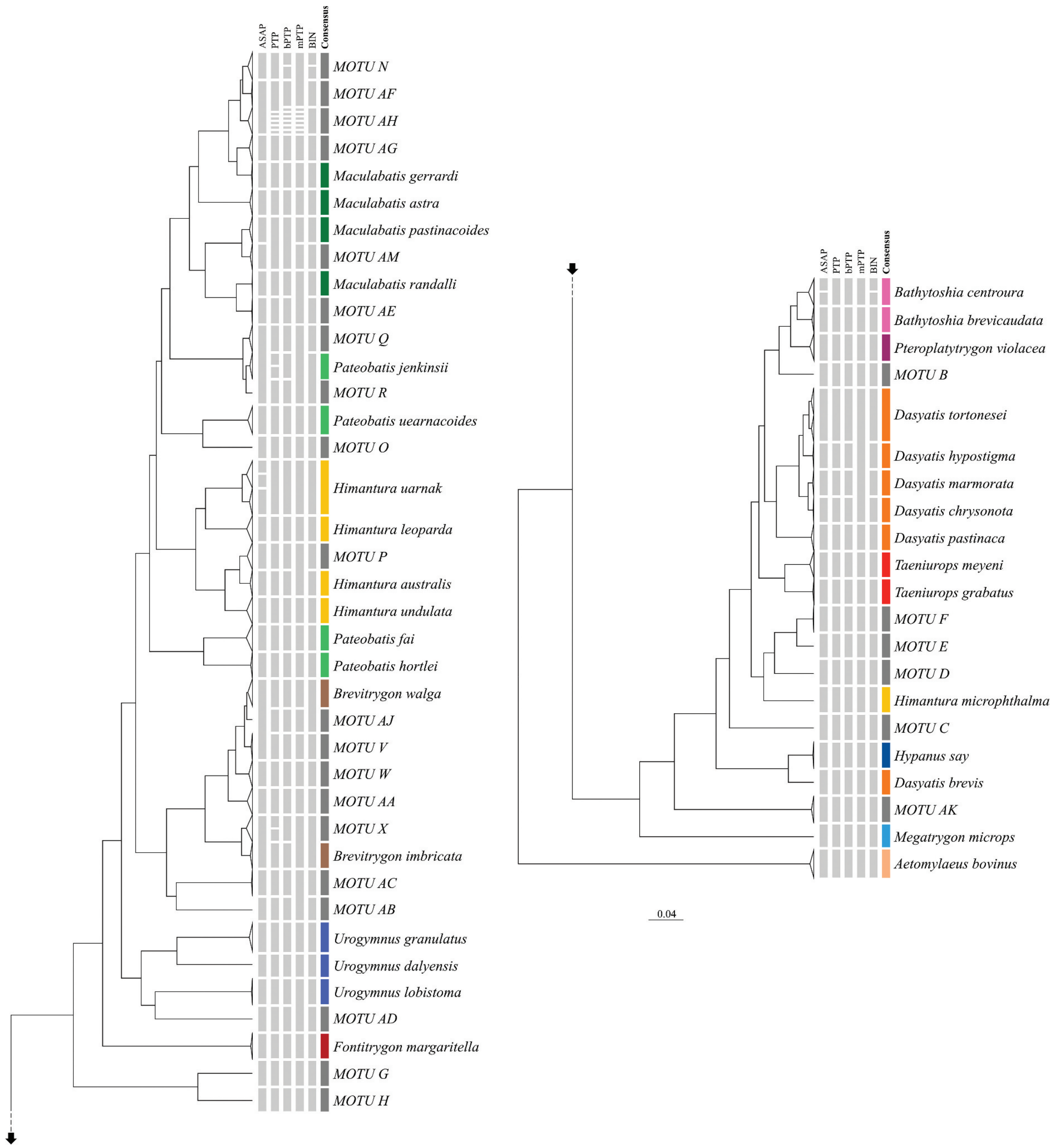

Figure 7. YSP Bayesian tree reconstruction for COI is shown as two subtrees; the subtree on the left continues with the subtree on the right. In the columns on the right, light grey bars report for each species the attribution according to the different methods: ASAP, PTP, bPTP, mPTP and BIN. Coloured bars represent the consensus taxon according to the methods proposed. MOTU refers to taxa not corresponding to a known nominal species. Each genus is characterized by a different colour; MOTUs are marked in dark grey.

Furthermore, our results pointed out the possible occurrence of multiple species: cryptic, undescribed, and/or not characterized from a molecular point of view. Our analyses failed to attribute the divergent haplotypes to known species for *B. lata* (Figure 4; Figure 7, MOTUs X and AA), *D. pastinaca* (Figure 3; Figure 7, MOTU AK), and *P. violacea* (Figure 6; Figure 7, MOTU B). Surprisingly, we found criticalities also in *A. bovinus* (the outgroup), suggesting the occurrence of a possible cryptic species in the Senegalese waters (Figure 8, MOTU AP).

Likewise, eight and four MOTUs were found starting from *Himantura* spp. sequences in the COI and NADH2 datasets, respectively. In the genus *Maculabatis* (dark green label; Figures 7 and 8), our results suggest that at

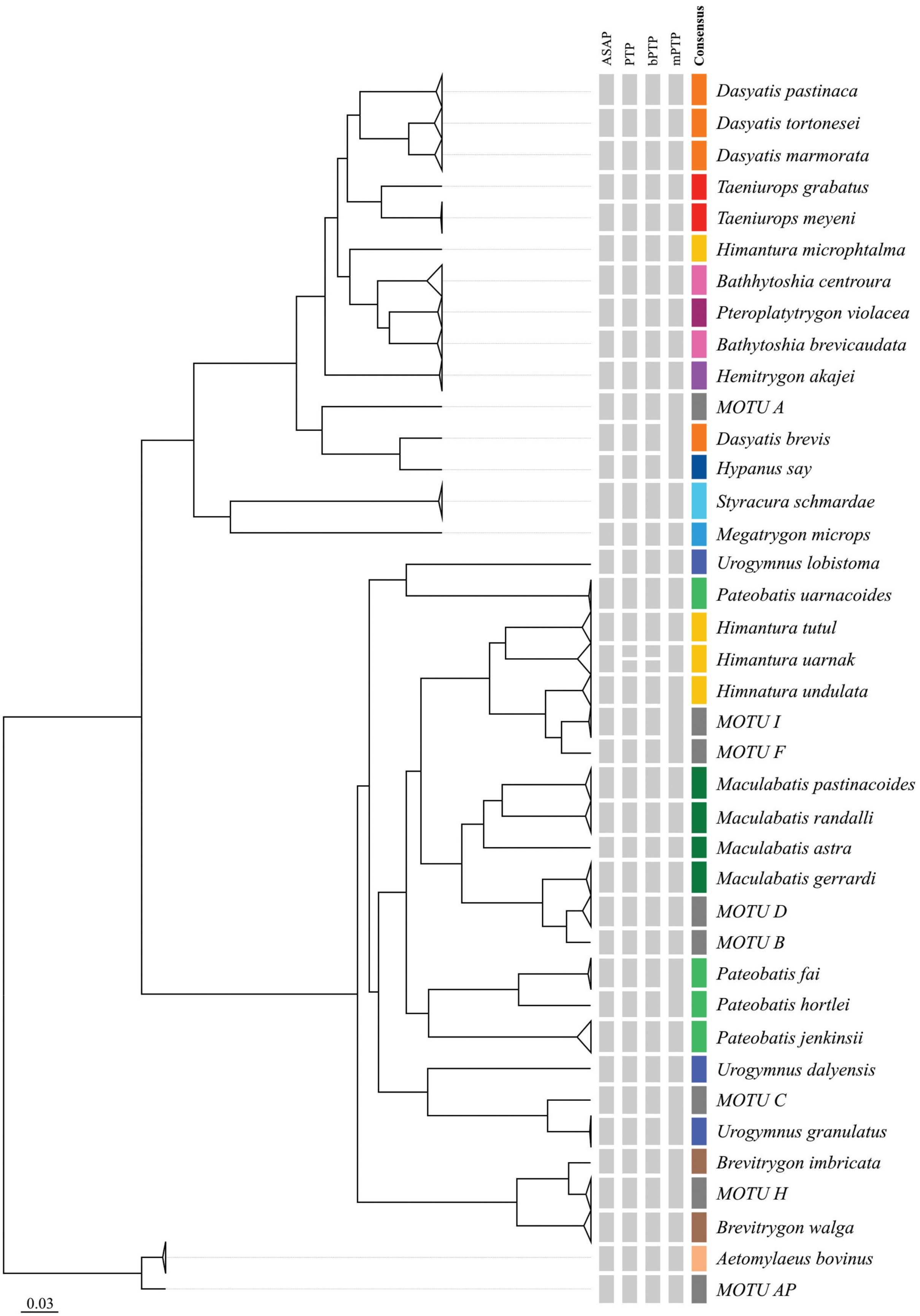

Figure 8. YSP Bayesian tree reconstruction for NADH2. In the columns on the right, light grey bars report for each species the attribution according to the different methods: ASAP, PTP, bPTP and mPTP. Coloured bars represent the consensus taxa according to the methods proposed. MOTU refers to taxa not corresponding to a known nominal species. Each genus is characterized by a different colour; MOTUs are marked in dark grey.

least six undescribed cryptic species occur. The genus *Brevitrygon* (brown label; Figures 7 and 8) should be enriched by the description of several new species.

Lastly, the results pointed out the occurrence of phylogenetic incongruences. As observed by Last et al. (2016) and Coelho (2017), we found a lack of monophyly in the genera *Dasyatis*, *Himantura*, and *Urogymnus*. Additionally, the sequences of the genus *Pateobatis* did not cluster together in both COI and NADH2 trees (green label; Figures 7 and 8). *Himantura microphthalma* (Chen, 1948) was placed outside of its putative genus group (yellow label; Figures 7 and 8), and was positioned instead near the genera *Dasyatis*, *Bathytoshia* and *Taeniurops*. This species was in the midst of a long taxonomic debate that is still ongoing; it was initially described as *Dasyatis microphthalmos* Chen 1948, subsequently attributed to *Himantura* by Compagno and Roberts (1982), and finally re-attributed to the genus *Dasyatis* by Manjaji-Matsumoto and Last (2006). *Eschmeyer's Catalog of Fishes* (Fricke et al. 2025) acknowledges the existence of taxonomic uncertainties with *H. microphthalma*, suggesting that the species should be recognized as *Dasyatis* but not excluding the possibility that it belongs to the genus *Telatrygon*. Similarly, *D. brevis* was placed near *H. say*. The urgent need to clarify the position of *Hypanus* after the genus's resurrection (van der Bank 2019; Davidson et al. 2022) was already underlined by Petean et al. (2020, 2024). Additionally, it was suggested that *D. brevis* and *Hypanus dipterurus* (Jordan & Gilbert, 1880) could be considered synonymous, giving strength to the attribution of *D. brevis* to the genus *Hypanus* (Miller et al. 2014). *Dasyatis pastinaca*, given the large genetic distance observed, could represent a lineage different from the other congeneric species despite its morphological likeness to other stingrays. Again, the distance observed between two *Himantura* groups, the first represented by *H. leoparda*, *H. tutul* and *H. uarnak*, and the second by *H. australis* and *H. undulata*, is similar to the genetic distances calculated between valid genera, suggesting the need to place them in distinct taxa. As concerns the genera *Pteroplatytrygon* (dark pink label; Figures 7 and 8) and *Bathytoshia* (pink label; Figures 7 and 8), they cluster close together, suggesting that they can possibly be merged into a single taxonomic group (i.e. *Bathytoshia*).

Conclusion

The current study expanded the geographical distribution of *D. tortonesei* by confirming for the first time that specimens of the species can be found in Sardinian waters (Figure 2). New, easy-to-use and resolutive identification keys are necessary to improve the possibility of correctly discriminating Mediterranean stingrays, in particular the Tortonese's stingray from the common stingray. In this way, it will be possible to obtain reliable information about the distribution and abundance of these species, key data for the planning of sound conservation measures. Furthermore, more research will be required to evaluate the genetic variability, population structure and connectivity of Mediterranean stingrays.

Results presented during this work underlined uncertainties also about the species of the genus *Bathytoshia*, supporting the existence of a single species corresponding to the analysed sequences of *B. lata* and *B. centroura*. In particular, according to the original description of the species, we propose to use the original name of *B. centroura* for individuals from the Atlantic Ocean, Mediterranean Sea and Indian Ocean (Garman 1913; Ebert & Stehmann 2013; Weigmann 2016; Carpenter & De Angelis 2016) and references therein). However, the lack of public sequences hampered detailed comparisons and the application of species delimitation analyses, and for this reason it cannot be ruled out that a second distinct species could exist. Future studies are necessary to understand whether *B. lata* may be considered a valid species present in the Pacific Ocean as reported in the original description (Garman 1913), or if it has a broader geographical distribution.

Additionally, our results also revealed the presence of several MOTUs and taxonomic incongruencies that require additional research: (i) to uncover possible new species that have not yet been identified, and (ii) to address unresolved phylogenetic relationships. There is still much more research needed to learn about the rays hidden in the shadows (Glaus et al. 2024).

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Authors contribution

CRediT: **Simone Di Crescenzo:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Validation, Visualization, Writing – original draft, Writing – review & editing; **Chiara Pani:** Data curation, Formal analysis, Methodology, Visualization, Writing – review & editing; **Blondine Agus:** Writing – review & editing; **Andrea Bellodi:** Writing – review & editing; **Riccardo Porceddu:** Writing – review & editing; **Cristina Porcu:** Writing – review & editing; **Maria Cristina Follesa:** Funding acquisition, Resources, Writing – review & editing; **Rita Cannas:** Funding acquisition, Resources, Validation, Visualization, Writing – review & editing.

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Data availability statement

The data that support the findings of this study are available in the supplementary material of this article. Accession numbers of deposited COI (PX462887–PX462898) and NADH2 (PX512454–PX512473) haplotype sequences are reported in Table SM1 for each analysed sample and highlighted in bold.

Ethical approval

Samples of stingray individuals analysed in the present work were obtained from commercial and scientific fisheries. The activity was conducted under the observation of the Regulation of the European Parliament and the Council for fishing in the General Fisheries Commission for the Mediterranean (GFCM) Agreement area and amending Council Regulation (EC) No. 1967/2006. This Regulation is de facto the unique authorization needed to conduct this type of activity.

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