

Morphological and Molecular Evidence Reveals the Longnose Skate *Zearaja brevicaudata* (Marini, 1933) to be a Senior Synonym of *Dipturus lamillai* Concha, Caira, Ebert & Pompert 2019

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Longnose skates have great economic importance in South American fisheries, and in order to preserve them, it is important to have a well-defined taxonomic status of their species. *Dipturus lamillai* was recently described for Malvinas Islands waters based on morphological and molecular comparisons with *Zearaja chilensis*. Although *D. lamillai* has been compared with several congeneric species, it was not properly compared with the morphologically similar *Zearaja brevicaudata*, the most abundant longnose skate in the Southwest Atlantic. Here, these species were compared by morphological and molecular analyses in order to evaluate their conspecificity. Linear morphometric variables of holotype and paratypes of *D. lamillai* and 69 specimens of *Z. brevicaudata* were compared and investigated using Principal Component Analysis. In addition, thorn patterns, denticle distributions, color, and clasper morphology were compared. No body proportions or other single character that could differentiate *D. lamillai* from *Z. brevicaudata* were found. Molecular analyses comprised of the comparison of the Cytochrome oxidase subunit I (*COI*) and the NADH dehydrogenase subunit 2. The results of the Maximum Likelihood (ML) carried out for each molecular marker showed that sequences from *D. lamillai* clustered together with those of *Z. brevicaudata*, and the molecular distance determined by Kimura two-parameter were lower than the expected for different species. Additionally, the Automatic Barcode Gap Discovery method and the Bayesian implementation of the Poisson tree processes were carried out with *COI* sequences to explore species limits, and their results were consistent with ML analyses. In summary, the results obtained showed that there are no morphological or molecular differences between these nominal species of the valid skate genus *Zearaja*, leading to the conclusion that they are conspecific. Therefore, we designated *Z. brevicaudata* as a senior synonym of *D. lamillai*.

Key words: Integrative taxonomy, Longnose skates, Rajiformes, Synonyms, Southwest Atlantic.

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BACKGROUND

Most of the recognized members of the family Rajidae (*sensu* Last et al. 2016a) were initially assigned to the genus *Raja*, which was later found to consist of multiple subgenera (McEachran and Dunn 1998). In their morphologically based phylogenetic study of the group, the family Rajidae (at subgeneric level) was found to consist of 15 genera; five of these were elevated from the subgenera of *Raja* (*i.e.*, *Amblyraja*, Malm 1877; *Dipturus* Rafinesque, 1810; *Leucoraja* Malm, 1877; *Okamejei* Ishiyama, 1958; and *Rajella* Stehmann, 1970). These taxa remain in use at the generic level but there have been several amendments to the classification. *Dipturus* was described by Rafinesque (1810), who characterized the genus by the presence of two dorsal fins in the tail, and the absence of a caudal fin, and considered *Dipturus batis* (as *Raja batis* Linnaeus, 1758) the type species. Whitley (1939) described *Zearaja* Whitley, 1939, providing only the description of the type species *Zearaja nasuta*, which was originally described as *Raja nasuta* Müller and Henle, 1841. Considering the neurocranium morphology of this species, Stehmann and Bürkel (1990) considered *Zearaja* as a synonym of *Dipturus*. Last and Gledhill (2007) resurrected the genus *Zearaja* from synonymy with *Dipturus*, including their new species *Zearaja maugeana* Last and Gledhill, 2007, as well as *Raia chilensis* Guichenot, 1848 and *Raja nasuta*. Some taxonomic issues have been addressed with the elevation of *Zearaja* from *Dipturus* based mainly on morphological data (Last and Gledhill 2007) and supported by unpublished molecular data (Naylor, Chondrichthyan Tree of Life Project). The main morphological characteristic that differentiates *Zearaja* species from other rajid skates is the unique combination and anatomical configuration of components forming the clasper (Last and Gledhill 2007). Earlier, Naylor et al. (2012) had called into question the validity of the genus *Zearaja* based on molecular data (NADH2), stating that the genus *Dipturus* would be monophyletic only if the genus *Zearaja* was included within *Dipturus*. In contrast, Vargas-Caro (2017), by means of a complete mitochondrial genome analysis, found that both genera (*Dipturus* and *Zearaja*) were monophyletic. More recently, Concha et al. (2019), based on a molecular analysis of the mitochondrial gene NADH dehydrogenase subunit 2 (NADH2) and morphological features of the clasper, synonymized *Zearaja* with *Dipturus*, relocating all *Zearaja* species within *Dipturus*. Unfortunately, the Concha et al. (2019) molecular tree (Concha et al. 2019: fig. 13) is extremely limited in the number of *Dipturus* taxa represented (only 2 of 38 species of *Dipturus* treated in Last et al. 2016a, and

not including the type species, *Raja batis*). Hence, this study does not factor in the rich diversity of *Dipturus* as defined by McEachran and Dunn (1998, 29 species) when the subgenus was first elevated to generic status. However, this nomenclatural decision is not widely accepted and was not adopted in the revision of skates and batoids of the world, which maintains the validity of the genus *Zearaja*, mostly based on clasper morphology and the particular importance of this structure in the taxonomy of skates (Last et al. 2016a). In support of this argument, comprehensive molecular analyses from the Chondrichthyan Tree of Life Project, including the type species of the genus, confirm the paraphyly of *Dipturus* as defined by Concha et al. (2019). This taxon includes *Zearaja* and several presently undefined genera (Naylor unpubl. data; Awruch et al. 2021). Hence, to avoid creating additional confusion in the literature, we have chosen to follow the nomenclature used in the most recent taxonomic review of the group (Last et al. 2016a). Moreover, the Catalog of Fishes currently presents *Zearaja* as a valid genus (Fricke et al. 2022).

Skates of the genera *Zearaja* Whitley, 1939 and *Dipturus* Rafinesque, 1810 (Rajidae) are medium to large-sized skates, characterized by a rhombic disc and a medium to long snout with stiff rostral cartilage (Last et al. 2016a). They occur from cold temperate waters to tropical seas, and on continental shelves and slopes where they have their greatest diversity. Until 2018, eight longnose skate species had been reported in South American waters: *D. argentinensis* Díaz de Astarloa, Mabragaña, Hanner and Figueroa, 2008, *D. bullisi* (Bigelow and Schroeder, 1962), *D. ecuadoriensis* (Beebe and Tee-Van, 1941), *D. leptocauda* (Kreff and Stehmann, 1975), *D. mennii* Gomes and Paragó, 2001, *D. teevani* (Bigelow and Schroeder, 1951), *D. trachyderma* (Kreff and Stehmann, 1975) and *Z. chilensis*. Weigmann (2016), based on White (pers. comm. 2014), also assigned *D. argentinensis* to *Zearaja*, considering molecular data provided in the original description of the species. Nonetheless, the main morphological characteristic that differentiates *Dipturus* and *Zearaja* species is clasper morphology, which is still unknown for *D. argentinensis*. Therefore, we continue using the original designation until further studies of the clasper morphology are provided. Within the last few years, two more species had been added to the Southwest Atlantic (SWA): *Z. brevicaudata* (Marini, 1933) and *D. lamillai* Concha, Caira, Ebert and Pomper, 2019. The former is distributed in the SWA, from southern Brazil (34°S) to southern Argentina (Gabbanelli et al. 2018). Although *Z. brevicaudata* was described in 1933 (under the name *Raia brevicaudata* Marini, 1933), it was identified as *Z. chilensis* for almost a century, since it was placed in synonymy

with this species by Norman (1937). Recently, *Raia brevicaudata* was resurrected from synonymy with *Z. chilensis* from the Southeast Pacific (SEP) and placed in *Zearaja* based on an integrative taxonomic analysis including DNA barcode (Cytochrome oxidase subunit I, *COI*), external morphology and skeletal features (Gabbanelli et al. 2018). *Dipturus lamillai* was described, based on morphological and molecular analyses of the mitochondrial gene NADH2, from specimens collected around the Malvinas/Falkland Islands in the SWA (Concha et al. 2019). According to the authors, individuals of this species had previously been identified as *Z. flavirostris* by Naylor et al. (2012). Concha et al. (2019) also redescribed *Z. chilensis* and designated a neotype for this species. The description of *D. lamillai* was largely based on the comparison of both morphological and molecular features of *Z. chilensis* from Chile. Concha et al. (2019) also compared, at the morphological level, *D. lamillai* with three congeners reported from waters off Malvinas/Falkland Islands: *D. argentinensis*, *D. leptocauda*, and *D. trachyderma*. However, a comprehensive comparison with the recently resurrected *Z. brevicaudata*, the most abundant and widespread longnose skate species from the SWA, was not provided. Indeed, Concha et al. (2019) only compared the coloration of *D. lamillai* with that of the holotype of *Z. brevicaudata* from the original description of Marini (1933) and with the coloration described by Gabbanelli et al. (2018). In addition, Concha et al. (2019) stated that morphometric comparisons between *D. lamillai* and *Z. brevicaudata* were difficult to make. The reasons the authors provided were that measurements presented by Gabbanelli et al. (2018) combined juvenile, subadult, and adult specimens of both sexes and this did not allow comparisons of the same size or sex of both species. In addition, Concha et al. (2019) pointed out that “although measurements are presented for the holotype specimen, that specimen is a juvenile female (32.4 cm in TL) and those measurements are not comparable to those for the holotype of *D. lamillai* sp. nov., which is an adult male.” Since Gabbanelli et al. (2018) and Concha et al. (2019) did not use the same genetic markers (*COI* and NADH2, respectively), molecular comparisons between both species have not been made. Interestingly, Concha et al. (2019) pointed out that the two complete mitochondrial genomes registered in GenBank under nos. KJ913073 and KF648508 (both identified as *Z. chilensis*) represented *Z. chilensis* and *D. lamillai*, respectively. One of the mitochondrial sequences (KJ913073) was obtained from a specimen collected in Chile (Vargas-Caro et al. 2014). The other sequence (KF648508), was obtained from a raw fillet sample of *Z. chilensis* collected from a restaurant in Korea (Jeong

and Lee 2016). As expected, the mitochondrial genome contains, in addition to other genes, both the *COI* and the NADH2 genes, that could be also used to identify the specimen KF648508.

Given the economic importance of longnose skates in SWA fisheries (Agnew et al. 2000; Colonello et al. 2002; Massa et al. 2004a b; Cedrola et al. 2005; Estalles et al. 2011; Arkhipkin et al. 2012) and their vulnerability to overexploitation (Stevens et al. 2000; Frisk et al. 2001; Dulvy et al. 2014), it is necessary to make a thorough taxonomic comparison between *Z. brevicaudata* and *D. lamillai* in order to determine whether both correspond to the same or different species. Therefore, the objective of this study is to compare these two nominal species through an integrative morphometric and molecular analysis.

MATERIALS AND METHODS

Examined material

The examined material is listed in table S1. Given the impossibility of analyzing the type material as a consequence of global COVID-19 pandemic travel restrictions, data of *D. lamillai* were taken from Concha et al. (2019). These data constituted linear morphometric variables, expressed as a percentage of total length (TL), taken from the holotype (FA-46: mature male, 787 mm TL) and paratypes (FA-39: mature male, 915 mm TL, FA-47: mature female, 942 mm TL) of *D. lamillai* and were compared to the data from 69 specimens of *Z. brevicaudata* (216–1017 mm TL), including the holotype of *Raia brevicaudata* (MACN-ict- 569). Forty-seven of these specimens were previously analyzed in Gabbanelli et al. (2018), and the rest were revised for this study, (Table 1, Table S1). The maturation stage of individuals was assigned and they were classified as neonates, juveniles, subadults and adults. Females were dissected after examination to observe oviductal glands and oocytes size, and clasper calcification was registered in males following Paesch and Oddone (2008) and Colonello and Cortés (2014). Some of these specimens are stored at collections in different institutions, including: Museo Argentino Bernardino Rivadavia, Buenos Aires, Argentina (MACN), Universidad Nacional de Mar del Plata, Mar del Plata, Argentina (UNMDP), Instituto Nacional de Desarrollo Pesquero, Mar del Plata, Argentina (INIDEP), Instituto de Ciencias del Mar, Barcelona, España (IIPB). Specimens not stored in collections were analyzed under the field code RM (Table S1). For comparative purposes, data from 15 specimens of *Z. chilensis* were taken into account, and some of the specimen are stored

at the ichthyological collection of the Museo Nacional de Historia Natural, Santiago de Chile (MNHN) (Table S1).

Morphological analyses

Morphological comparisons between *D. lamillai* and *Z. breviceaudata* were carried out. The variables were taken following the same measurement methodology of Last et al. (2008). Relationships between variables that were included in the diagnosis of *D. lamillai* were calculated for *Z. breviceaudata* (from the original measurements in mm), and compared with the results obtained by Concha et al. (2019). A normalization technique to scale the data that exhibited allometric growth was employed following Leonart et al. (2000). This method was derived from theoretical equations of allometric growth and completely removes all information related to size, not only scaling all individuals to the same size, but also adjusting their shape to a standard form according to allometry. Total length (TL) was used as the independent variable, while the remaining measurements were considered dependent variables. TL₀ represents a reference value of size (570 mm for this study, regarding the TL of the specimens included in the analysis) to which all individuals were either reduced or amplified (Leonart et al. 2000; Konan et al. 2010; Orlando et al. 2015; González-Castro et al. 2016; Mabrugaña et al. 2020). After transformation, a new matrix was constructed, which contained the corrected matrices for each species, and a Principal Component Analysis (PCA) was performed with the transformed variables using the FactoMineR package (Lê et al. 2008) in the software

R 4.0.2 (R Core Team 2020). Data from neonates were excluded and only data from juveniles and adults were considered for this analysis. Measurements of 14 juveniles and one adult of *Z. chilensis* were also included in the analyses for comparative purpose. In addition, thorn patterns and denticle distribution following Gravendeel et al. (2002), color, and clasper morphology following Hulley (1972) of the two nominal species were compared.

Molecular analyses

COI analyses

Sequences of Cytochrome oxidase subunit I (COI) of *D. argentinensis* (n = 7), *Z. breviceaudata* (n = 25), *Z. chilensis* (n = 10), *Z. nasuta* (Banks, 1841) (n = 15), *D. lamillai* (n = 14) were included in the molecular analyses. In addition, the placement of the COI sequence from the complete mitochondrial genome of *Z. chilensis* sequenced by Jeong and Lee (2016) (KF648508) was analyzed. Sequences of *D. argentinensis*, *Z. breviceaudata* and two sequences of *Z. chilensis* belong to Laboratorio de Biotaxonomía Morfológica y Molecular de Peces, Instituto de Investigaciones Marinas y Costeras (CONICET-UNMdP), all sequences from *D. lamillai* belong to Chondrichthyan Tree of Life Project, all sequences of *Z. nasuta* and eight sequences of *Z. chilensis* were downloaded from Barcode of Life Data System (BOLD), and a sequence of KF648508 was downloaded from GenBank. Sequences of COI and NADH2 used in this work are listed in the tables S2 and S3, respectively. Sequences were aligned by Muscle (Edgar 2004) in the

Table 1. Data of specimens of *Zearaja breviceaudata* and *Z. chilensis* analyzed

	Stage	Sex	N	TL range
<i>Zearaja breviceaudata</i>	Neonates	M	2	216–228
		F	1	254
	Juveniles	M	24	310–617
		F	25	324–705
	Subadults	M	4	645–776
		F	2	815–942
	Adults	M	3	787–884
		F	8	760–1017
<i>Zearaja chilensis</i>	Juveniles	M	8	294–534
		F	6	305–507
	Adults	M	1	896

F: female, M: male, N: number of specimens, TL: total length, in mm.

software MEGA X (Kumar et al. 2018). A best-fit model of nucleotide evolution was estimated using Akaike information criterion in MEGA X and was determined to be Kimura two-parameter (K2P). Distance divergences were calculated using K2P. A Maximum Likelihood (ML) was carried out for cluster analyses using K2P, and 1000 bootstrap pseudoreplicates were conducted to estimate node support values. A sequence of the rajid species *Amblyraja doellojuradoi* (Pozzi, 1935), from the Argentine Sea, was used as the outgroup. Distance divergences and ML analyses were performed in MEGA X. The *COI* sequences of *D. lamillai* and KF648508 were compared with BOLD, and BIN assignment was analyzed. The BIN analysis clusters barcode sequences algorithmically to create Operational Taxonomic Units (OTUs) that show high concordance with species. Species limits were also explored using the Automatic Barcode Gap Discovery method (ABGD) (Puillandre et al. 2012) and the Bayesian implementation of the Poisson tree processes (bPTP) (Zhang et al. 2013). The ABGD automatically finds the distance at which a barcode gap occurs and sorts the sequences into putative species based on this distance. Therefore, as with BIN analysis, ABGD is applicable as an independent tool without an a priori species hypothesis, and it provides insight into whether the taxonomic identification based on morphological features has any genetic support. The ABGD was run with the default settings (P min = 0.001, P max = 0.1, steps = 10, X relative gap width = 1.5, Nb bins = 20) and K2P distance on the web server <https://bioinfo.mnhn.fr/abi/public/abgd/>. The bPTP uses nucleotide substitutions to estimate intra- and interspecific processes. It identifies the shift among intra- and interspecific processes by using one parameter for coalescence and another for speciation. It was conducted at the web server <https://species.h-its.org/ptp/>; the parameters for the run were 100,000 MCMC generations, a thinning interval of 100 and 10% of burn-in.

NADH2 analyses

Sequence data from the protein-coding gene NADH dehydrogenase subunit 2 (NADH2) was generated for *Z. brevicaudata* in order to compare them with those of *D. lamillai*. Tissue samples of *Z. brevicaudata* collected in the SWA, Argentine Sea ($n = 4$) were stored in 95% ethanol prior to DNA extraction using the E.Z.N.A. Tissue DNA Kit (Omega Bio-Tek, Inc., Georgia USA). Universal primers were used to amplify the mitochondrial NADH2 fragment by Polymerase Chain Reaction (PCR) for all samples prior to purification and Sanger sequencing, following Naylor et al. (2012). Sequences of NADH2 provided by

Concha et al. (2019) were downloaded from Genbank (MK613969, MK613970, MK613971, MK613972, MK613973, MK613967, MK613966, MK613968) as well as the NADH2 sequence from the complete mitochondrial genome sequenced by Jeong and Lee (2016) (KF648508). Also, other sequences identified as *D. lamillai* belonging to the Chondrichthyan Tree of Life Project were taken into account. For comparative purposes, sequences of *D. argentinensis*, *Z. chilensis*, *Z. nasuta*, and *D. olseni* (Bigelow and Schroeder, 1951) (as outgroup) were included in the following analyses (sequence data in Table S3). DNA sequences were aligned and distance divergences were calculated using K2P. Maximum Likelihood (ML) analysis of clusters was carried out using the GTR+G model, as it was determined to be the best model under Akaike criterion and 1000 rapid bootstrap replicates. These analyses were performed in MEGA X (Kumar et al. 2018).

RESULTS

Morphological analyses

Morphometrics

The specimens of *Z. brevicaudata* analyzed ranged from 216 to 1017 mm TL, and included neonates, juveniles, and adults. Those of *D. lamillai* ranged from 485 to 1140 mm, but measurements were given only for the adult holotype and paratypes, which ranged from 787 to 940 mm TL (Table 2).

Table 2 summarizes measurements expressed as percentages of TL of *D. lamillai* and *Z. brevicaudata*. No variables distinguish *D. lamillai* from *Z. brevicaudata*, since all measurements of *D. lamillai* are included within the range of *Z. brevicaudata*. On the other hand, table 3 summarizes the relationships between variables included in the diagnosis and description of *D. lamillai* for both species. In the same way, all respective values of *D. lamillai* are within the range of *Z. brevicaudata*. Moreover, the values are the most similar when only adult ranges of the two species are compared (Table 2 and 3). Ratios of tail length in relation to TL for males and females of *Z. brevicaudata* range from 38.4 to 40.3% TL and from 36.3 to 38.4% TL, respectively, similar to the data for *D. lamillai* by Concha et al. (2019) (37.9% and 38.4% TL for two males, 35.1% TL for one female). The PCA generated for standardized body measurements, including *Z. brevicaudata*, *Z. chilensis*, and *D. lamillai*, produced three eigenvalues greater than 1 (data not shown). The first three principal components explained 44.3% of the variance of morphometric data (24.8%, 12.6%, and

6.8%, respectively). The PCA allowed a clear separation of individuals from the SEP and the individuals from the SWA when comparing PC1 vs. PC2, and with a small degree of overlap when comparing PC1 vs. PC3 (Fig. 1). Specimens from the SEP corresponded to *Z. chilensis* and specimens from the SWA corresponded to *Z. brevicaudata* and *D. lamillai*. Specimens of *Z. brevicaudata* and *D. lamillai* appeared together in one group, and there was no differentiation between them. Moreover, the three individuals of *D. lamillai* appeared scattered between specimens of *Z. brevicaudata* (Fig. 1a). Correspondingly, both nominal species differed from *Z. chilensis* by the same characteristics: larger preorbital length, greater snout-spiracle distance, larger head length (dorsal and ventral), greater spiracle length and the distance between them, greater snout

to cloaca distance, larger preoral and prenasal length, and shorter cloaca to tail tip distance (Table 4). The variables with higher loadings that differentiate SWA specimens from those of the SEP are related to snout length. This strongly suggests that both *D. lamillai* and *Z. brevicaudata* have a longer snout and a shorter tail than specimens of *Z. chilensis*.

Thorn and denticle patterns

Thorn data of *D. lamillai* (Concha et al. 2019) were compared with those of *Z. brevicaudata* (Table 5). The thorn pattern of both species is similar, with thorns in orbital, nuchal, dorsal and caudal regions in all individuals, and in malar and alar regions in adult males. Moreover, the number of thorns present in each body

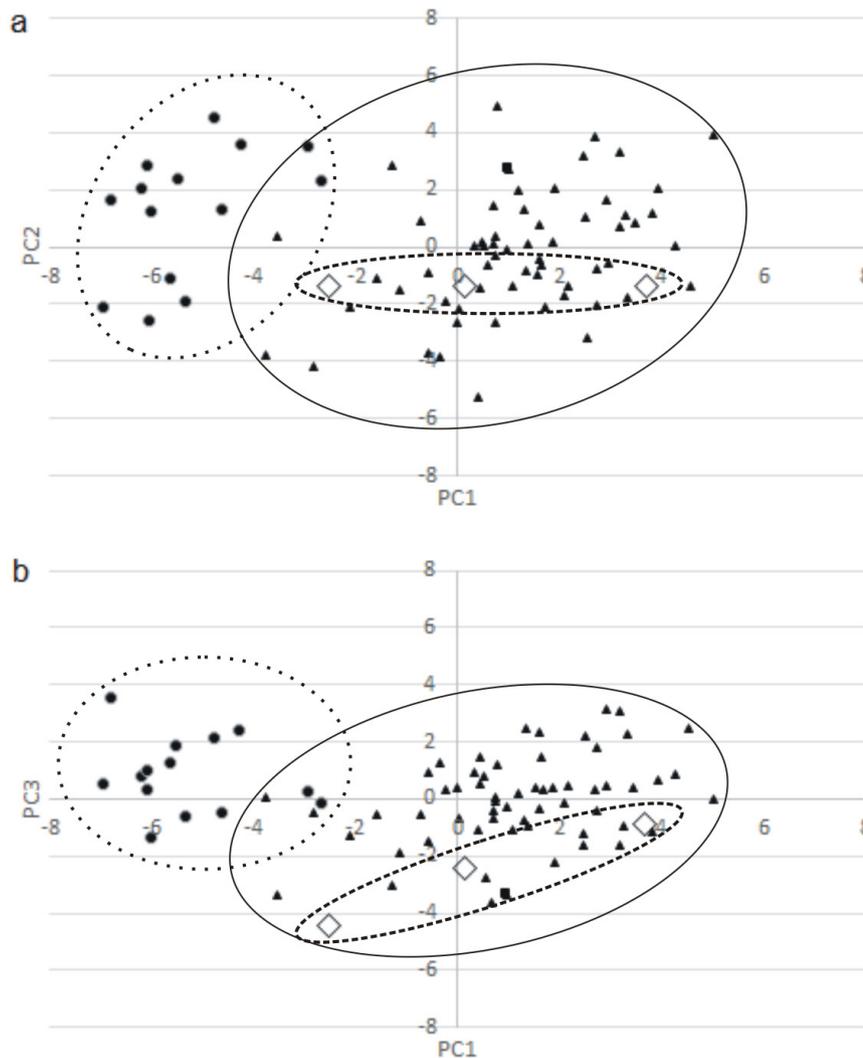


Fig. 1. Principal component analysis based on morphological data expressed as percentage of total length. a) PC1 vs. PC2 b) PC2 vs. PC3. PC1: first principal component, PC2: second principal component, PC3: third principal component. ▲, ellipse with whole line: *Zearaja brevicaudata*; ■, holotype of *Raia brevicaudata*; ●, ellipse with dotted line: *Z. chilensis*; ◇, ellipse with dashed line: *Dipturus lamillai*.

Table 2. Measurements for *Dipturus lamillai* (3 types) and *Zearaja brevicaudata* (holotype and 68 non-type specimens) expressed as percentages of total length. Clasper measurements are given for adult males of *Z. brevicaudata* ($n = 3$)

	<i>Dipturus lamillai</i>				<i>Zearaja brevicaudata</i>						
	Holotype FA-46	Paratype FA-39	Paratype FA-47	Holotype MACN-ict- 569	Total range			Adults			
				mm	%	Range	Mean	SD	Range	Mean	SD
Sex	M	M	F	F							
Total length (TL, mm)	787	915	940	324.0	–	216.0–1017.0	–	–	760.0–1017.0	–	–
Measurements in % TL											
Disc width	75.2	73.2	78.9	250.0	77.2	61–83.1	77.3	3.3	74.3–82.3	77.3	2.8
Direct disc length	63.8	59.3	65.5	200.0	61.7	55.3–74.8	62.3	2.5	60–74.8	64.6	4.3
Snout to maximum width	41.7	39.1	45.2	122.0	37.7	32.3–42	37.3	2.3	35–41.4	39.1	1.8
Direct preorbital length	20.2	19.7	23.4	62.0	19.1	16.5–24	20.5	1.3	18.7–24	21.2	1.4
Snout to spiracle	23.5	23.7	26.3	81.5	25.2	21.8–30.1	25.9	1.4	24–30.1	26.8	1.6
Dorsal head length	27.2	25.4	28.2	84.4	26.1	23–31.1	27.3	1.4	26.2–31.1	28.3	1.4
Orbit diameter	2.8	3.6	2.7	14.6	4.5	3–4.8	3.8	0.4	3.4–4.8	3.8	0.5
Orbit and spiracle length	5.0	5.8	5.4	18.7	5.8	4.9–6.6	5.5	0.3	5.2–6.6	5.6	0.4
Spiracle length	2.7	2.1	2.7	7.4	2.3	1.7–3.1	2.5	0.3	1.9–3.0	2.6	0.4
Distance between orbits	6.4	6.4	6.6	16.1	5.0	4.6–6.8	5.6	0.5	5.7–6.8	6.2	0.4
Distance between spiracles	7.8	8.1	7.7	25.1	7.8	6.6–8.9	7.3	0.4	7.4–8.9	7.9	0.5
Distance snout to cloaca	61.6	61.7	64.9	183	56.5	49.1–69	59.4	3.3	60.3–69	63.4	2.5
Cloaca to tail tip	38.4	38.3	35.1	140.3	43.3	36.3–49.5	40.9	2.6	36.3–42	38.1	1.9
Preoral length	19.1	17.5	22	64.2	19.8	16.4–23.5	20.1	1.4	17.8–23.4	20.1	1.5
Direct prenasal length	17.9	16.7	20.7	60.7	18.7	15.1–21.7	18.5	1.2	16.5–21.7	18.7	1.4
Direct ventral head length	36.3	35.0	32.7	110.4	34.1	30–40.4	35.6	1.8	35.2–40.4	37.1	1.6
Mouth width	9.3	9.7	10.3	30.6	9.4	8.3–11	9.5	0.4	9.4–10.6	9.9	0.3
Distance between nostrils	9.4	9.6	9.7	30.4	9.4	7.6–10.6	9.5	0.5	9.3–10.6	9.8	0.4
Nasal curtain length	4.9	4.7	5.0	13.3	4.1	3.8–6	4.7	0.5	4.8–6	5.3	0.4
Nasal curtain maximum width	10.2	11.4	10.0	31.4	9.7	8.3–11.1	9.8	0.6	9.9–11.1	10.4	0.4
Width of first gill opening	2	1.5	2.1	4.5	1.4	0.9–2.5	1.7	0.2	1.4–2.1	1.7	0.2
Width of fifth gill opening	1.7	1.7	2.0	5.0	1.5	1.2–2.2	1.6	0.2	1.3–1.9	1.6	0.2
Distance between first gill openings	15	16.4	16	53.5	16.5	13.8–17.8	16.3	0.9	15.6–17.8	16.9	0.8
Distance between fifth gill openings	9.4	9.8	11.1	34.0	10.5	8.4–11.8	10.3	0.8	8.8–11.8	10.6	1.0
Length of anterior pelvic lobe	14.2	13.4	13.3	42.7	13.2	10.8–15.3	12.9	1.1	10.8–13.8	12.1	1.0
Length of posterior pelvic lobe	20.7	20.4	17.8	49	15.1	11.4–20.2	15.7	1.4	14.5–20.2	17.1	2.1
Pelvic base width	9.4	9.6	10.9	38.1	11.8	9.9–18.5	13.9	1.8	12–18.5	15.6	2.1
Tail width at axis of pelvic fin	4.1	4.0	3.9	13.5	4.2	2.7–5	4.0	0.5	3.2–4.6	4.0	0.5
Tail height at axis of pelvic fin	2.4	2.4	2.3	13.2	4.1	1–4.1	2.4	0.4	2.1–3.1	2.5	0.3
Tail width at tail midlength	2.6	3.0	2.7	7.6	2.3	1.4–3.2	2.4	0.4	1.6–3	2.5	0.5
Tail height at tail midlength	1.4	1.7	1.4	5.3	1.6	0.8–2.1	1.4	0.2	1.2–1.7	1.5	0.2
Tail width at base of D1	2.5	2.4	2.4	9.1	2.8	1.2–3	2.2	0.4	1.6–2.3	2.2	0.4
Tail height at base of D1	1.5	1.5	1.5	4.7	1.5	0.8–1.7	1.4	0.2	1.1–1.6	1.4	0.2
D1 base length	5.1	5.3	4.3	18.3	5.6	4.1–6.9	5.2	0.4	4.2–5.8	5.0	0.4
D1 height	4.3	3.2	3.9	11.4	3.5	2.8–4.8	3.8	0.4	3.4–4.7	4.0	0.5
Origin of D1 to tail tip	14.3	12.6	12.9	55.6	17.2	11.4–21.5	15.8	1.7	12.7–16.8	14.4	1.3
Origin of D2 to tail tip	6.6	6.9	7.1	33.4	10.3	5.1–14.2	9.2	1.5	5.7–9.7	8.1	1.4
Caudal fin length	2.3	2.4	2.3	13.2	4.1	1.7–7.6	4.0	1.0	1.7–5.2	3.3	1.1
Caudal fin height	0.7	0.6	0.2	2.7	0.8	0.1–1.2	0.7	0.2	0.5–1	0.6	0.2
Post cloaca clasper length	31.6	29.4	-	-	-	-	-	-	29.1–30	-	-
Cloaca to clasper insertion	11.9	11.4	-	-	-	-	-	-	12.1–12.3	-	-

SD: standard deviation; M: male, F: female, D1: first dorsal fin; D2: second dorsal fin.

region coincides between both species. Specimens of *D. lamillai* had three rows of tail thorns, as described for *Z. breviceaudata*. In the female paratype of *D. lamillai* a single lateral tail thorn above the lateral tail fold was found, and it was also observed in *Z. breviceaudata*. The female paratype of *D. lamillai* was described as having a continuous median row of thorns on trunk and tail, as well as parallel trunk thorns behind the shoulder girdle (Concha et al. 2019). Eight specimens, seven females and one male (688–1017 mm TL), of *Z. breviceaudata* were found to have a thorn pattern similar to that observed in the female paratype of *D. lamillai*. All of them presented parallel rows of thorns on the body, and two adult females presented median trunk thorns (Fig. 2). Moreover, the same sexual dimorphism was observed in parallel trunk thorns and lateral tail thorns, which had a wider range in females. With respect to malar thorns, adult males of *Z. breviceaudata* presented 3–6, while adult males of *D. lamillai* presented 6–10.

The denticle pattern described for *D. lamillai* (Concha et al. 2019) matched the pattern of *Z. breviceaudata* (Gabbanelli et al. 2018). Individuals from both nominal species presented denticles on the head, dorsally from tip of snout to the posterior part of neurocranium, ventrally from tip of snout to about level of first gill slits, around cloaca in adults, on the anterior margin of the dorsal fins, and completely covering the caudal fin. In addition, both nominal species did not have denticles on the pectoral and pelvic fins, and on

the tail, either ventrally or dorsally.

Coloration

Concha et al. (2019) indicated a coloration for *D. lamillai* different from the pattern described for *Z. breviceaudata* by Gabbanelli et al. (2018). Nevertheless, similarities in the descriptions were observed: both nominal species presented an ocellus on the base of each pectoral fin and the area flanking the rostral cartilage was translucent. Additionally, pale fuzzy circles were described for *Z. breviceaudata*, which were consistent with the light brown spots also described for *D. lamillai* as well. Moreover, new specimens of *Z. breviceaudata* were analyzed for the present study and some of them presented a coloration similar to that described for the female paratype of *D. lamillai* (Fig. 3).

Clasper morphology

Claspers of both nominal species did not differ in their shape and showed the same external components. However, two additional components of the claspers were described for *D. lamillai*: spur and slit (Concha et al. 2019). These components were not indicated for *Z. breviceaudata* (Gabbanelli et al. 2018). Nevertheless, after re-examination of the claspers of *Z. breviceaudata* the component spur and slit were both present. The spur is the external part of the dorsal terminal cartilage

Table 3. Relationships between measurements used in the diagnosis and description of *Dipturus lamillai*, based on the holotype (FA-46) and paratypes (FA-39, FA-47) of *D. lamillai* and specimens of *Zearaja breviceaudata* (n = 69). D1: first dorsal fin

		<i>Dipturus lamillai</i>	<i>Zearaja breviceaudata</i>	
		FA-46 (FA-39:FA-47)	Total range	Adults
Diagnosis	Preorbital snout length/distance between orbits	3.2(3.1:3.5)	2.9–4.3	3.1–3.6
	Orbit diameter/interorbital distance	0.4(0.6:0.4)	0.5–0.9	0.5–0.7
Description	Disc width/disc length	1.3(1.4:1.3)	1.2–1.4	1.2–1.3
	Preorbital snout length/orbit length	7.2(5.5:8.7)	1.1–6.6	4.5–6.6
	Preorbital snout length/interorbital distance	3.2(3.1:3.5)	2.9–4.3	3.1–3.6
	Spiracles/orbit diameter	1.1(1.7:1)	1.1–2.2	1.2–1.8
	Distance 1st gills/internasal distance	1.6(1.7:1.7)	1.4–2	1.6–1.9
	Distance 5th gills/internasal distance	1(1:1.1)	0.6–1.3	0.9–1.2
	Anterior lobe/posterior lobe	0.7(0.7:0.8)	0.6–1.1	0.6–0.8
	Cloaca to caudal fin-snout to cloaca	0.6(0.6:0.5)	0.6–2.2	0.6–0.7
	Width at pelvic fin axils/width at midlength tail	1.6(1.4:1.4)	1.1–2.8	1.3–2
	Width at pelvic fin axils/width at D1	1.6(1.7:1.6)	1.1–3.7	1.4–2.6
	Width at pelvic fin axils/height at pelvic fins axils	1.7(1.7:1.7)	1–4	1.2–1.8
	Width at pelvic fin axils/height at 1/2 tail	2.8(2.3:2.8)	1.4–3.8	2.5–2.9
	Width at pelvic fins axils/height D1	2.8(2.6:2.6)	2.1–4	2.3–3.4
D1 height/base length	1.2(1.1:1.1)	0.5–1.1	0.7–1	

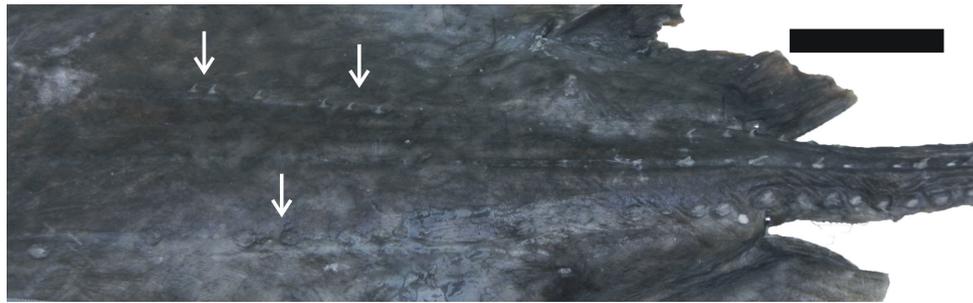


Fig. 2. Dorsal spinulation pattern of an adult female of *Zearaja brevicaudata* (RM 170, 943 mm TL). White arrows point the dorsal thorns. Scale bar = 50 mm.

Table 4. Variable loadings for the first three axes of a principal component analysis for standardized measurements of specimens of *Zearaja brevicaudata* and *Dipturus lamillai*. The highest loadings are indicated in bold. D1: first dorsal fin, D2: second dorsal fin

	PC1	PC2	PC3
Disc width	0.6	0.4	0.0
Direct disc length	0.6	0.2	0.2
Snout to maximum width	0.2	0.1	0.1
Direct preorbital length	0.9	0.0	0.1
Snout to spiracle	0.9	0.1	0.2
Dorsal head length	0.9	0.1	0.2
Orbit diameter	-0.2	0.3	-0.2
Orbit and spiracle length	-0.3	0.6	-0.1
Spiracle length	-0.3	0.5	0.2
Distance between orbits	0.2	0.3	-0.2
Distance between spiracles	0.3	0.4	-0.6
Snout to cloaca	0.9	0.2	0.0
Cloaca to tail tip	-0.9	0.0	0.2
Preoral length	0.9	0.0	0.1
Direct prenasal length	0.9	0.0	0.1
Direct ventral head length	0.3	0.6	0.5
Mouth width	-0.1	0.5	0.2
Distance between nostrils	0.2	0.6	0.1
Nasal curtain length	0.0	0.2	0.0
Nasal curtain maximum width	-0.3	0.5	0.1
Width of first gill opening	-0.3	0.3	0.2
Width of fifth gill opening	-0.2	0.4	0.0
Distance between first gill openings	-0.5	0.5	0.4
Distance between fifth gill openings	0.4	0.4	0.3
Length of anterior pelvic lobe	0.4	0.2	-0.1
Length of posterior pelvic lobe	-0.1	0.3	-0.3
Pelvic base width	0.5	0.3	0.0
Tail width at axis of pelvic fin	0.3	0.4	-0.3
Tail height at axis of pelvic fin	-0.1	0.4	-0.1
Tail width at tail midlength	-0.1	0.3	-0.6
Tail height at tail midlength	-0.2	0.5	-0.2
Tail width at base of D1 fin	-0.2	0.3	-0.6
Tail height at base of D1 fin	0.2	0.4	-0.5
D1 base length	-0.6	0.5	-0.1
D1 height	-0.1	0.5	0.1
Origin of D1 to tail tip	-0.7	0.2	0.3
Origin of D2 to tail tip	-0.6	0.2	0.3
Caudal fin length	-0.6	0.2	0.3

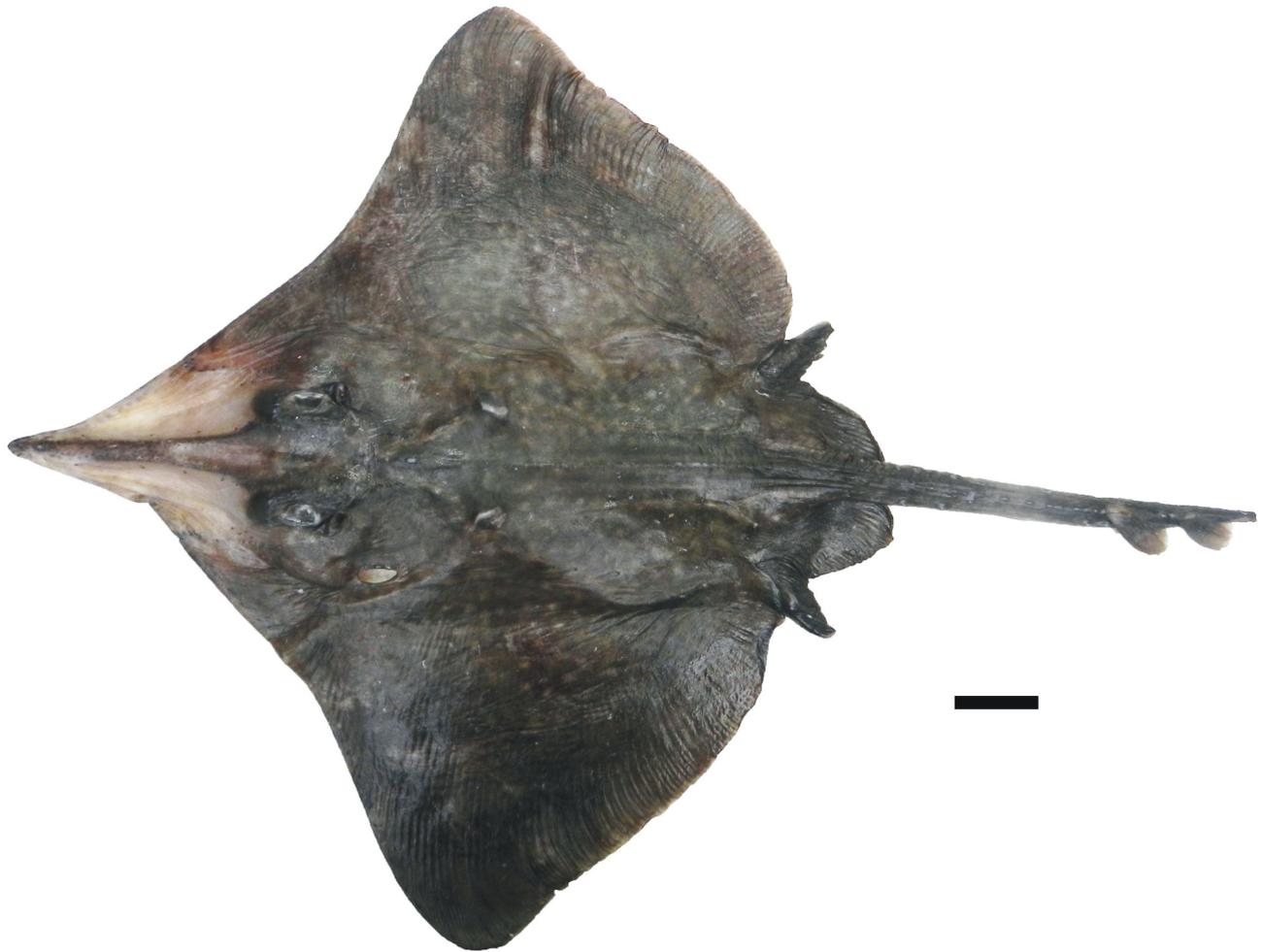


Fig. 3. Female specimen of *Zearaja brevicaudata* (RM 317, 427 mm TL) showing the same coloration pattern as female paratype of *Dipturus lamillai* (cf. Concha et al., 2019, fig. 7B). Scale bar = 50 mm.

Table 5. Thorn patterns of the holotype (FA-46) and paratypes (FA-39, FA-47) of *Dipturus lamillai* taken from Concha et al. (2019) and specimens ($n = 69$) of *Zearaja brevicaudata*

	<i>Dipturus lamillai</i>			<i>Zearaja brevicaudata</i>
	FA-46	FA-39	FA-47	Total range
Sex	M	M	F	both
Orbital thorns	5	5	6	2–7
Nuchal thorn*	1	1	1	1
Malar thorns**	6	10	-	3–6
Alar thorns**	10	18	-	12–16
Alar thorns longitudinal rows**	3	3	-	2–3
Median trunk thorns***	-	-	4	4–6
Parallel trunk thorns****	-	-	7 each side	3–13 each side (F) 1–3 each side (M)
Midline tail thorns	20	25	22	10–27
Lateral tail thorns	6 each side	6 each side	14 each side	1–20 each side (F) 1–5 each side (M)
Interdorsal thorns	3	2	2	1–3

*sometimes absent, **present in adult males only, ***present in adult females only, ****present in adult specimens only. F: females, M: males.

3 (dt3), and the slit is a narrow flap situated proximally in the glans, and in this case is situated above the dt3 (Fig. 4).

Molecular analyses

DNA Barcode analyses

The ML tree of the *COI* sequences revealed four well-defined cohesive clusters, corresponding to the following species involved in the analysis: *D. argentinensis*, *Z. breviceaudata*, *Z. chilensis*, and *Z. nasuta* (Fig. 5). Each cluster was supported by high bootstrap values (> 80). Results of the ML tree also showed that sequences from the Chondrichthyan Tree of Life project of specimens identified as *D. lamillai* and the specimen sequenced by Jeong and Lee (2016), identified by Concha et al. (2019) also as *D. lamillai*, clustered with individuals of *Z. breviceaudata*. K2P distance between sequences of both species ranged from 0 to 0.7%, with an average value of 0.2% (Table 6).

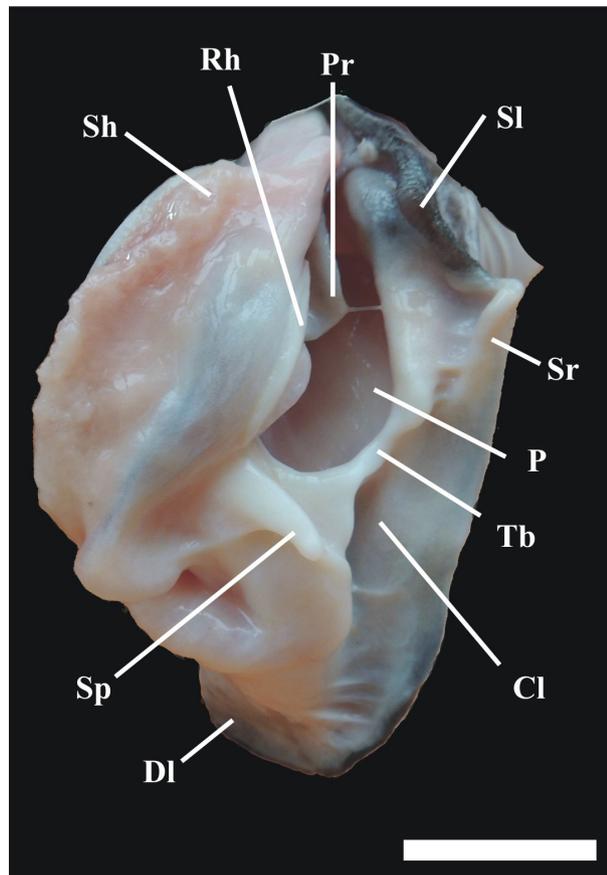


Fig. 4. External components of the clasper of a mature male of *Zearaja breviceaudata* (RM 186, 783 mm TL). Cl: cleft, Dl: distal lobe, P: pocket, Pr: pseudorhiphidion, Rh: rhiphidion, Sh: shield, Sl: slit, Sp: Spike, Sr: spur, Tb: terminal bridge. Scale bar = 30 mm.

When compared to the BOLD data base, sequences of *D. lamillai* and the sequence of KF648508 were included in the BIN AAB5856, together with *Z. breviceaudata* sequences. Sequences of *D. argentinensis*, *Z. chilensis* and *Z. nasuta* were included in BIN AAB5857 (Fig. 5a). The analyses of the ABGD resulted in seven partitions that ranged from 23 ($P = 0.0010$) to two candidate species ($P = 0.01$). From the first partition that presented 23 groups, the following two presented five candidate species ($P = 0.0016 - P = 0.0027$) which were consistent with the four cohesive clusters found in the ML tree and the outgroup, grouping *Z. breviceaudata* and *D. lamillai* sequences together (Fig. 5b). The bPTP analyses identified four OTUs: one attributed to *Z. breviceaudata* and *D. lamillai*, one to *Z. chilensis* and *Z. nasuta*, one to *D. argentinensis* and the last one to the outgroup *A. doellojuradoi* (Fig. 5c).

NADH2 analyses

Maximum likelihood analyses of NADH2 sequences revealed four clusters that corresponded to almost all the species involved (Fig. 6). Three clusters were composed of *D. argentinensis*, *Z. chilensis*, and *Z. nasuta*, respectively. Interestingly, the fourth cluster was composed of sequences of *D. lamillai* and *Z. breviceaudata*. Each cluster was supported by high bootstrap values (> 60). The K2P distance between both species, *D. lamillai* and *Z. breviceaudata*, ranged from 0 to 0.5% and the mean K2P distance between them was 0.1% (Table 7).

Synonymization of *D. lamillai* with *Z. breviceaudata*

Morphological and molecular comparisons between *Z. breviceaudata* and *D. lamillai* demonstrate that they are conspecific. Following the Principle of Priority of the International Code of Zoological Nomenclature (Art. 23, ICZN 1999), *D. lamillai* is placed as a junior synonym of *Z. breviceaudata*. Accordingly, an updated synonymy of *Z. breviceaudata* is presented as follows:

Raja breviceaudata Marini, 1933: 329: Rectificando errores ictiológicos, Physis 11, 328–332 [original description; holotype MACN-ict- 569].

Raja stabuliformis: Marini (1928).

Raja flavirostris: Norman (1937); Ringuélet and Aramburu (1971); Menni and López (1984); García de La Rosa (1998); Agnew et al. (2000); Wakeford et al. (2004).

Raja (Dipturus) flavirostris: Gosztanyi 1981; Menni 1971 1973; Menni et al. 1984.

Dipturus flavirostris: Menni and Stehmann (2000); Cedrola et al. (2005).

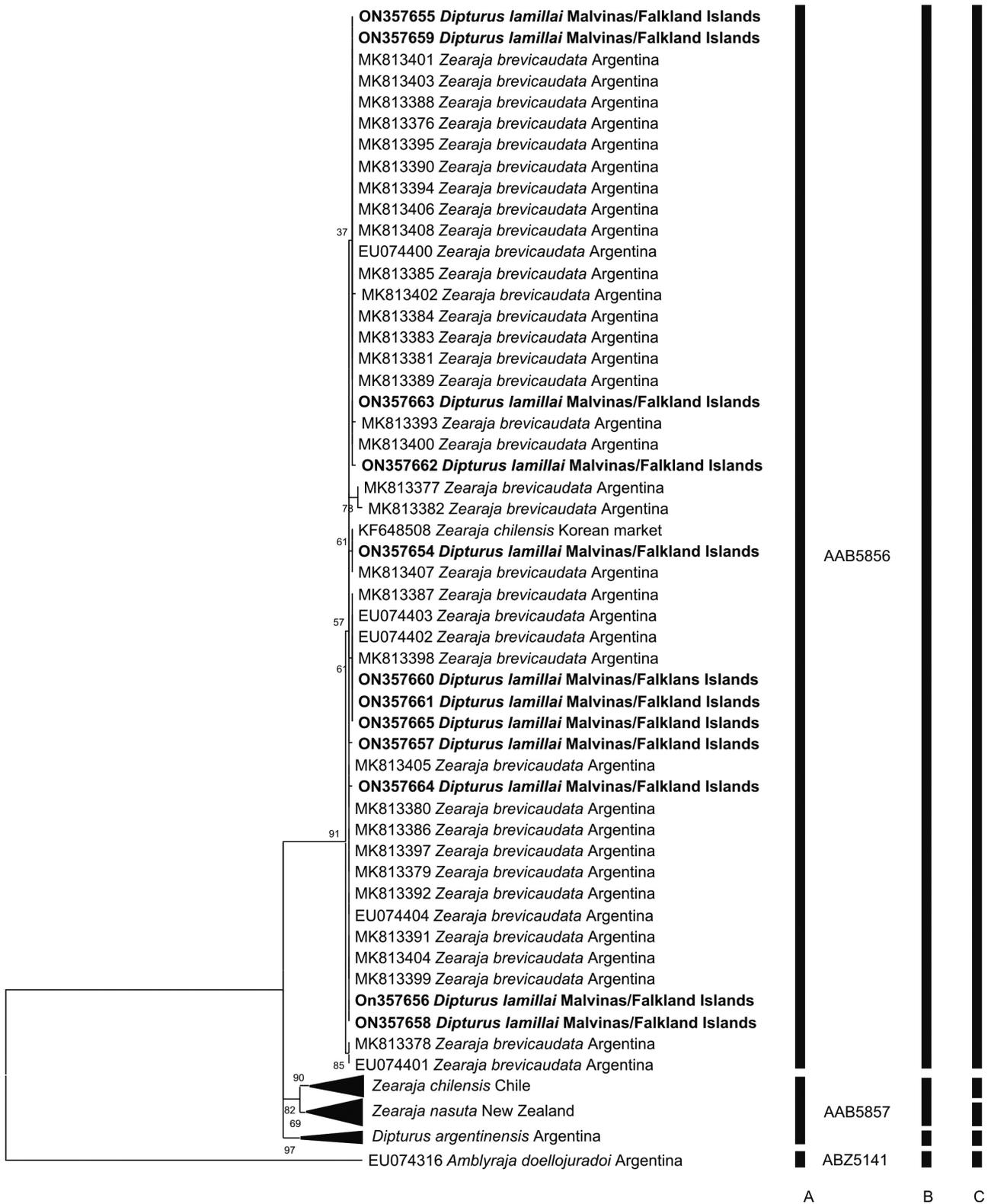


Fig. 5. Maximum Likelihood tree, produced with Cytochrome oxidase subunit I (*COI*) sequences of *Dipturus argentinensis*, *D. lamillai*, *Zearaja brevicaudata*, *Z. chilensis*, *Z. nasuta* and *Amblyraja doellojuradoi* as outgroup. Barcode Index Number assigned by Barcode of Life Datasystem (A) and the results of species delimitation analyses using bPTP (B) and ABGD (C) algorithms are shown as vertical bars on the right. *Dipturus lamillai* sequences are marked in bold.

Raja (Dipturus) chilensis: Lloris and Rucabado (1991); Pequeño and Lamilla (1993); Bizikov et al. (2004).

Dipturus chilensis: Cousseau et al. (2000 2007);

Lucifora et al. (2000); Soto and Mincarone (2001); Gomes and Picado (2001); Kohen Alonso et al. (2001); Nion et al. (2002); Sánchez and Mabrugaña (2002); García de la Rosa et al. (2004); Oddone et al. (2005);

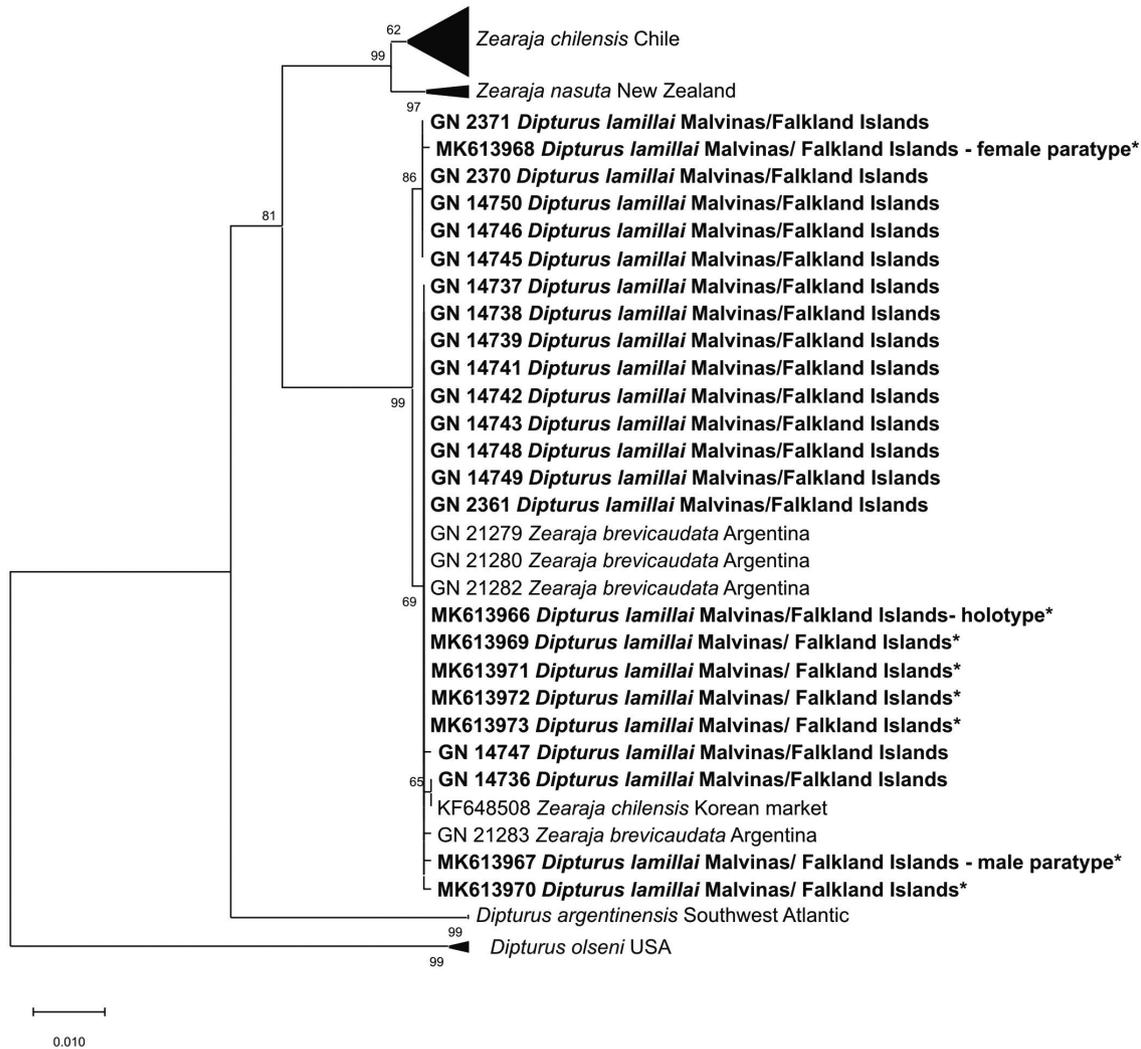


Fig. 6. Maximum Likelihood tree produced with NADH dehydrogenase subunit 2 (NADH2) sequences of *Dipturus argentinensis*, *D. lamillai*, *Zearaja brevicaudata*, *Z. chilensis*, *Z. nasuta* and *D. olseni* as outgroup. *Dipturus lamillai* sequences are marked in bold and sequences corresponding to the description of the species (Concha et al. 2019) are indicated with *.

Table 6. Intra- and interspecific K2P distance of the Cytochrome oxidase subunit I mitochondrial gene for *Dipturus argentinensis*, *D. lamillai*, *Zearaja brevicaudata*, *Z. chilensis* and *Z. nasuta*. Values in the diagonal correspond to intraspecific distance and the below ones to interspecific distance

	<i>Zearaja chilensis</i>	<i>Z. brevicaudata</i>	<i>Dipturus argentinensis</i>	<i>Z. nasuta</i>	<i>D. lamillai</i>
<i>Zearaja chilensis</i>	0.1	-	-	-	-
<i>Z. brevicaudata</i>	3.5	0.1	-	-	-
<i>Dipturus argentinensis</i>	1.7	3.3	0.1	-	-
<i>Z. nasuta</i>	0.9	3.4	1.8	0.3	-
<i>D. lamillai</i>	3.5	0.2	3.3	3.5	0.2

Díaz de Astarloa et al. (2008); Paesch and Oddone (2008); Estalles et al. (2011); Mabrugaña et al. (2011a); Colonello and Cortés (2014); Silveira et al. (2018).

Zearaja chilensis: Vargas-Caro et al. (2015) [in part]; Weigmann (2016) [in part]; Last et al. (2016a) [in part]; Last and Gledhill (2007); Mabrugaña et al. (2011b); Deli Antoni et al. (2012); Arkhipkin et al. (2012); Bovcon et al. (2013); Jeong and Lee (2016).

Zearaja flavirostris: Menni et al. (2010); Naylor et al. (2012); Izzo et al. (2017).

Dipturus lamillai Concha, Caira, Ebert and Pompert, 2019: 513 [original description; holotype: MNHNCL ICT 7531, paratypes: CAS 242403, MNHNCL ICT 7532]; Pompert et al. (2020).

DISCUSSION

The integrative morphometric, skeletal and molecular analyses carried out between individuals of *Z. breviceaudata* and *D. lamillai* show that these species are conspecific. Therefore, *D. lamillai* is designated, herein, as a junior synonym of *Z. breviceaudata*.

The conspecificity is firstly evidenced by the morphological similarities. Concha et al. (2019) stated that individuals of *D. lamillai* and *Z. breviceaudata* could not be compared due to the different sizes of the individuals analyzed. Concha et al. (2019) analyzed 41 specimens of *D. lamillai*, ranging from 485 to 1140 mm TL, comprising juvenile and adult specimens. However, the authors only provided measurements for three adult individuals, the holotype and two paratypes. Gabbanelli et al. (2018) reported morphometric data for 47 specimens of *Z. breviceaudata* from a neonate to adult individuals. Therefore, considering that Gabbanelli et al. (2018) provided morphological ranges for the complete life stages of the species, the range sizes of *D. lamillai* could have been compared, since adults were represented in the data provided for the resurrection of *Z. breviceaudata*. However, to make the morphometric analysis comparable and to avoid

any doubts about which part of the range (neonate, juvenile, or adult) overlaps between species, ranges of adult specimens of *Z. breviceaudata* were discriminated in the present paper. The results obtained from the morphometric comparisons evidenced the overlapping ranges between the two species. Concha et al. (2019) indicated differences between males and females of *D. lamillai* with respect to tail length, being longer in males (37.9% TL for the paratype and 38.4% TL for the holotype) than in females (35.1% TL for the paratype). These values match with the results obtained for *Z. breviceaudata* in the present study. On the other hand, no body proportions differentiating *D. lamillai* from *Z. breviceaudata* were found. Indeed, Concha et al. (2019) stated that *D. lamillai* differed from *D. argentinensis*, *D. leptocauda*, and *D. trachyderma* by the interorbital and interspiracular distances, as well as mouth width. However, all of these morphometric features overlap with those of *Z. breviceaudata*.

Thorn patterns of the specimens described as *D. lamillai* were consistent with those of *Z. breviceaudata*. Few differences were found, and they are most likely ascribed to intraspecific variation. The female paratype of *D. lamillai* presented a dorsal thorn pattern that had not been described in the resurrection of *Z. breviceaudata* by Gabbanelli et al. (2018). However, an equivalent thorn pattern was found in eight individuals analyzed in the present paper. Furthermore, this pattern had previously been described for *Z. breviceaudata* (as *Z. flavirostris*) by Izzo et al. (2017) in an analysis of the conspecificity of individuals from the SWA with different thorn pattern.

The only difference between *D. lamillai* and *Z. breviceaudata* indicated by Concha et al. (2019) was the color pattern. In this respect, it is known that coloration is sensitive to environmental influences (Leible 1988). Moreover, individuals of the same skate species may have a different coloration, and two different species may overlap in their coloration patterns (McEachran and Matheson 1985; Mabrugaña 2007; Weigmann 2017). Indeed, *Zearaja* skates can be highly variable

Table 7. Intra- and interspecific K2P of the NADH dehydrogenase subunit 2 mitochondrial gene for *Dipturus argentinensis*, *D. lamillai*, *Zearaja breviceaudata*, *Z. chilensis* and *Z. nasuta*. Values in the diagonal correspond to intraspecific distance and the below ones to interspecific distance

	<i>Dipturus argentinensis</i>	<i>Zearaja chilensis</i>	<i>D. lamillai</i>	<i>Z. nasuta</i>	<i>Z. breviceaudata</i>
<i>Dipturus argentinensis</i>	0	-	-	-	-
<i>Zearaja chilensis</i>	4.8	0.1	-	-	-
<i>D. lamillai</i>	5.4	2.9	0.2	-	-
<i>Z. nasuta</i>	5.2	1.0	3.4	0.3	-
<i>Z. breviceaudata</i>	5.4	2.9	0.1	3.4	0

in coloration, with *Z. nasuta* varying in its reticulation pattern, spotting and sometimes lacking ocelli (Last, unpubl. data). Since this characteristic is so variable, it is useless as the only diagnostic characteristic for species discrimination. According to Concha et al. (2019), the dorsal surface of *D. lamillai* is brownish with lighter spots and reticulations, ranging from simple (holotype) to complex (female paratype). On the other hand, according to Gabbanelli et al. (2018) the coloration of *Z. brevicaudata* is grayish on the dorsal surface except on the snout, which is yellowish-white on both sides of the rostrum. Herein, similarities between the descriptions have been observed. Moreover, the “complex pattern” observed in the *D. lamillai* female paratype (Concha et al. 2019) was found in specimens of *Z. brevicaudata* analyzed in the present study. Differences in descriptions could be due to the presence of a species with variable coloration, from brownish to grayish (similar to observations in other *Zearaja* species). However, it is important to note that the pale fuzzy circles described by Gabbanelli et al. (2018) match the lighter spots and reticulations found by Concha et al. (2019).

Clasper morphology has been widely used in skate taxonomy, as their claspers exhibit a large number of external and skeletal features that are important in species discrimination and classification (e.g., Leigh-Sharpe 1924; Ishiyama 1958; Stehmann 1970; Hulley 1972; Leible 1988; Weigmann et al. 2015; Last et al. 2016b; Moreira et al. 2017). The external and skeletal components of the claspers of *Z. brevicaudata* were fully described (Gabbanelli et al. 2018), whereas the clasper description of *D. lamillai* was based solely on the external components (Concha et al. 2019). The latter authors did not compare the clasper morphology of *D. lamillai* with that of *Z. brevicaudata*. Here, we compared the external morphology of the claspers from the description of *D. lamillai* (Concha et al. 2019) with that of *Z. brevicaudata* and found no differences.

The synonymy proposed here is strengthened by the molecular results. *COI* sequences of specimens previously identified as *D. lamillai* were compared with those of *Z. brevicaudata* through a Maximum Likelihood (ML) analysis. Also, the *COI* sequence of the complete mitochondrial genome KF648508 identified as *D. lamillai* by Concha et al. (2019) by means of the NADH2 molecular marker was included. Our results show that the *COI* sequences of the specimens identified as *D. lamillai* cluster together with those of *Z. brevicaudata*, and are identical to one sequence of this species. This is consistent with the results obtained through the species delimitation analyses (bPTP and ABGD) that grouped *Z. brevicaudata* and *D. lamillai* together. *Zearaja chilensis* and *Z. nasuta* were

grouped together in the bPTP analyses, but contrary to *Z. brevicaudata* and *D. lamillai*, these species do not share a cluster or group in the ML and the ABGD analyses, respectively. Moreover, the results of an ML tree generated with the NADH2 marker shows that sequences from specimens employed to describe *D. lamillai* cluster together with those of *Z. brevicaudata*. Coinciding with results obtained by *COI* analyses, NADH2 sequences of *D. lamillai* are identical to those of *Z. brevicaudata*.

Taxonomy is the most fundamental discipline in biodiversity research, building the foundation for other areas of knowledge, including conservation, given that without an accurate identification of the species, other areas of research could be compromised (Thomson et al. 2018; Lücking 2020). Many chondrichthyan species have been considered widespread, even though few differences between populations existed. In those cases, a careful comparison between populations is necessary in order to determine if the same species inhabits several places, or if it corresponds to different species (Last 2007), as happened with *Z. chilensis*. The recent resurrection of *Z. brevicaudata* from synonymy with *Z. chilensis* (Gabbanelli et al. 2018) has important implications for species conservation. The current taxonomy indicates two different species (not one as regarded before) with more restricted distributions. *Zearaja brevicaudata* has been subject to intense fishery exploitation in South America for many decades. It is an important target species due to its large body size. In order to deploy effective conservation measures and to effectively manage fisheries, it is crucial to have an accurate understanding of taxonomy. An example of the importance of good taxonomy involves *Merluccius patagonicus* Lloris and Mantallanas, 2003, which corresponds to a junior synonym of the common hake, *M. hubbsi* Marini, 1933 (Lloris and Matallanas 2003; Díaz de Astarloa et al. 2011). Unfortunately, until the synonymy of the two species was carried out, *M. hubbsi* was exploited under the name of *M. patagonicus*. In landings, the maximum allowable catch of *M. hubbsi* was not reached, but its populations were overexploited since it was being captured under another name (EUMOFA 2018). The case for *Z. brevicaudata* and *D. lamillai* is similar, with the added concern that the life history characteristics of chondrichthyan species make them even more vulnerable to fishery exploitation (Dulvy et al. 2017). Recently, *D. lamillai* was assessed by the IUCN as “Least Concern” (Pompert et al. 2020). The results obtained herein indicate that this assessment is inappropriate as *D. lamillai* corresponds to *Z. brevicaudata*. It is important to recognize that if management policies are adopted based on the assessment that *D. lamillai* is distinct, it

will confound our assessments of the population status of *Z. breviceaudata* which has recently been assessed as “Vulnerable” (Pollom et al. 2021). Unfortunately, the Covid-19 pandemic prevented our examination of the type material for the current work. This is a task that must be done in the future when safe travel becomes possible again. However, considering the importance of taxonomy in properly assessing the conservation status of *Z. breviceaudata*, the most exploited skate species in the Southwest Atlantic, the synonymization of *D. lamillai* with *Z. breviceaudata* is timely.

CONCLUSIONS

The present study combined morphological and molecular analyses, with the implementation of both *COI* and *NADH2* genes, that allowed the integrative comparison between *Z. breviceaudata* and *D. lamillai*, and consequently, their synonymization. It demonstrated the importance of accurate taxonomic research and the impact it may have on species conservation. In this sense, this research contributes baseline information to the conservation of a fishery resource by clarifying taxonomic issues within the longnose *Zearaja* skates occurring off the coasts of South America.

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Supplementary materials

Table S1. Data of specimens of *Zearaja brevicaudata* and *Zearaja chilensis* examined for the present study. F: female, M: male, TL: total length, given in mm, UM: uncatalogued material stored at Laboratorio de biotaxonomía morfológica y molecular de peces, IIMyC (CONICET-UNMdP). (download)

Table S2. Sequences information of the Cytochrome oxidase subunit I mitochondrial gene used in the present paper, corresponding to the following species *Dipturus argentinensis*, *Z. brevicaudata*, *Z. chilensis*, *Z. nasuta*, and *Amblyraja doellojuradoi*. BOLD: Barcode of Life Data System, PN: pending number. (download)

Table S3. Sequence information of the NADH dehydrogenase subunit 2 mitochondrial gene, used in the present paper, corresponding to the following species: *Dipturus argentinensis*, *Z. brevicaudata*, *Z. chilensis*, *Z. nasuta* y *D. olseni*. PN: pending Number. (download)