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A cryptic species of *Ensis* (Bivalvia: Pharidae) from the southeastern Pacific coast revealed by geometric morphometric methods

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Summary: A new cryptic species of *Ensis* from the Pacific coast of South America based on geometric morphometrics is revealed. *Ensis macha* (Molina, 1782) is one of the most important shellfish resources in South America. It was historically reported from San Matías Gulf, Argentina in the Atlantic Ocean to the Peruvian coast in the Pacific. A recent study analysed the intraspecific variation of this species along its distribution range and the genetic results indicated the presence of cryptic diversity. Two evolutionary clades were found: a southern clade (from cold-temperate waters) and a northern clade (from warm-temperate waters). New results based on geometric morphometrics supported the description of *Ensis loboi* n. sp. for the northern clade. The southern clade retains the name due to type locality of *E. macha* in Chiloé, Chile. The description of *Ensis loboi* n. sp. for the southeastern Pacific Ocean has important implications for future studies focused on fisheries management and biogeographical radiation of the group.

Keywords: Pharidae; Chile; Peru; Pacific Ocean.

Una especie críptica de *Ensis* (Bivalvia: Pharidae) de la costa sudeste del Pacífico revelada por morfometría geométrica

Resumen: *Ensis macha* (Molina, 1782) es uno de los recursos marisqueros más importantes de América del Sur. En este trabajo se describe una nueva especie críptica de *Ensis* que habita las costas del Pacífico de América del Sur, la cual fue revelada mediante la aplicación de morfometría geométrica. Históricamente *E. macha* fue reportada desde el Golfo San Matías, Argentina hasta las costas del Perú. Un estudio reciente analizó la variación intraespecífica de esta especie a lo largo de su rango de distribución y los resultados genéticos indicaron la presencia de diversidad críptica. Se encontraron dos clados evolutivos: un clado del sur (de aguas templadas frías) y un clado del norte (de aguas templadas cálidas). Nuevos resultados basados en morfometría geométrica 2D apoyaron la descripción de *Ensis loboi* n. sp. para el clado norte. El clado sur conserva el nombre debido a la localidad tipo de *E. macha* en Chiloé, Chile. La descripción de *Ensis loboi* n. sp. para el Océano Pacífico sureste tiene implicaciones importantes para futuros estudios enfocados en el manejo de pesquerías y la radiación biogeográfica del grupo.

Palabras clave: Pharidae; Chile; Perú; Océano Pacífico.

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INTRODUCTION

The family Pharidae currently includes 5 subfamilies and 14 genera. These are Pharinae H. and A. Adams, 1856 (9 species in 3 genera), Cultellinae Davies, 1935 (more than 25 species in 6 genera), Siliquinae Bronn, 1862 (15 species, 1 genus), Pharellinae Stoliczka, 1870 (7 species in 2 genera) and Novaculininae Ghosh, 1920 (5 species in 2 genera) (Cosel 2009, Coan and Valentich-Scott 2012, Cosel and Gofas 2019). Usually, the members of this group of bivalves have medium-to-large shells that are cylindrical in cross section and quadrate to ovate in outline. Some species show laterally compressed shells with terminal (*Ensis*) to subterminal (*Siliqua*, *Cultellus*) umbos. The exterior surface of the shell is characterized by commarginal ribs or irregular growth striae. The ligament is external and opisthodetic, and the hinge shows one vertical cardinal and one horizontal cardinal in the right valve and two vertical cardinals and two horizontal cardinals in the left valve. No lateral teeth are present in this family. Finally, the anterior adductor muscle scar is clearly larger than the posterior one. The mantle cavity organs are characterized by a siphon with variable length, short to long, separate or fused at the base, and a large foot, laterally compressed and truncate.

Taxonomic studies related to the family Pharidae have been carried out in several regions (Bloomer 1906, Urk 1964, 1966, 1971, 1972, 1980, 1986, Cosel 2009), and the latitudinal species richness was recently tested by Saeedi et al. (2017). For the southern tip of South America, only *Ensis macha* (Molina, 1782) has been historically mentioned in the literature (Carcelles 1944, Carcelles and Williamson 1951, Castellanos 1970). More recently, this species has been included in several lists of taxa and compendiums (Zelaya 2016, Valentich-Scott et al. 2020, Giacomino and Signorelli 2021). The reported distribution range of *Ensis macha* goes from the San Matías Gulf (40°S) in the Atlantic Ocean to the northern coast of Peru (8°S) in the Pacific (Zaixso et al. 2015, Paredes et al. 2016, Márquez et al. 2017). However, a recent study based on genetic data (COI mitochondrial and 856 nuclear genes) revealed the presence of two clades along the Pacific coast of South America (Márquez et al. 2020). They were designated as northern and southern clades. The northern clade is mainly distributed in the Peruvian biogeographic province (a warm-temperate region), from Peru (8°S) to the Chilean coast at around 37°S, while the southern clade is distributed along the Magellan province (a cold-temperate region) from Chiloé (40°S) on the Pacific coast to northern Patagonia on the Atlantic coast (40°S) (Fig. 1, Table 1).

Márquez et al. (2020) analysed the variation in external shell shape (outlines) using an elliptic Fourier analysis. They found that the two clades showed an overlapping morphospace, although there was a slight separation trend. The genetic distances reported by Márquez et al. (2020), plus new results based on landmark-based geometric morphometrics (GM), allowed the formal descriptions of a new species of Pharidae from the Pacific coast of South America. In order to maximize the separation between clades, 2D landmark-based GM was performed to analyse inner shell shape variation. Biogeographical implications related to the presence of two valid species of *Ensis* in the eastern Pacific coast of South America are discussed.

Table 1. – Sampling locations.

Species	Locations	Lat/long	n
Ensis macha (Molina, 1782)	Puerto Lobos, Argentina	42°00'S 65°04'W	57
	Caleta Carolina, Argentina	44°54'S 65°36'W	56
	El Porvenir, Chile	53°17'S 70°21'W	51
	Ancud, Chile	41°52'S 73°48'W	46
	Niebla, Chile	39°52'S 73°23'W	64
Ensis loboi n. sp.	Trujillo, Peru	08°06'S 79°01'W	2
	Dichato, Chile	36°37'S 72°57'W	49
	Tubul, Chile	37°13'S 73°26'W	45
Total			370

MATERIALS AND METHODS

Sample collection

The specimens were collected throughout the entire geographic distribution range of the South American razor clam, *Ensis*, from San Matías Gulf (41°34'S) in the Atlantic Ocean to Trujillo in the Pacific Ocean (08°06'S; Table 1). This study is compliant with the CBD and Nagoya protocols. All material was examined and compared with the specimens assigned to the new species. An updated distribution range for each valid species is illustrated (Fig. 1). The examined specimens were deposited in the Invertebrate Collection of IBIOMAR (CNP-Inv).

Geometric morphometrics

A total of 370 specimens, 274 from the southern clade and 96 from the northern clade were photographed with the inner side upwards. Following Márquez et al. (2017), the inner shell shape variation was studied using landmark-based GM and multivariate statistics. Twelve landmarks (2D configuration) were captured to examine shape variation of the internal muscle scars and pallial lines (Fig. 2). Procrustes analysis (Rohlf and Slice 1990) was used to remove rotation, translation and scale effects of the raw landmark coordinates. Centroid size (CS) was calculated as the square root of the sum of the square distances from the landmarks to the CS which they defined (Zelditch et al. 2004) and was used as a proxy for shell size. Multivariate regression (pooled within-site) between shape variables and CS values was calculated to evaluate and correct the positive allometry. To capture the shape components that maximized the separation between species, a discriminant function was calculated. Finally, the differences in mean shell shape between species were ana-

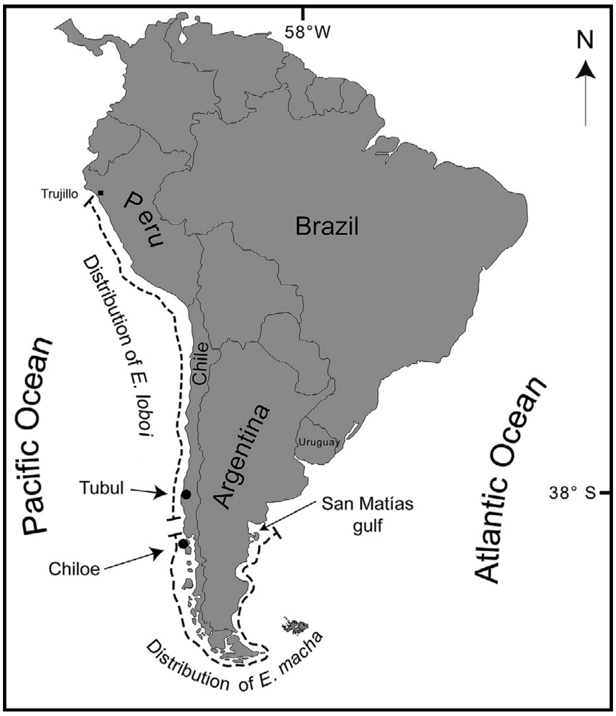

Fig. 1. – Map showing the distribution range of *Ensis loboi* n. sp. and *E. macha*. The type locality for each species is indicated with black dots. The black square indicates the location of the new material examined here and also the extreme of its distribution.

lysed by a T2 Hotelling test with 1000 permutations, and a re-sampling procedure (leave-one-out-cross-validation) was performed to estimate the percentage of misclassification to each species (Johnson and Wichern 2007). All GM analyses were conducted in MorphoJ, version 1.07a (Klingenberg 2011).

RESULTS

Geometric morphometrics

The independence between the Procrustes coordinates and the CS values was rejected (P<0.0001). Allometry explained 2.62% of the variation, so the residuals were used as the new allometric-free shell shape variables for subsequent analyses. Discriminant analysis showed that the shell shape range was different between the southern and northern clades. The mean inner shell shapes of the clades were significantly different (T2=761.07, p<0.0001, Mahalanobis distances= 3.27) (Fig. 3). The mean shell shape of the southern clade shows an anterior retraction and an expansion of the posterior part with a reduction of the anterior adductor muscle scar and the anterior and posterior retractor muscle scar of the foot in comparison with the mean shell shape of the northern clade (Fig. 3). The cross-validation function, based on the Mahalanobis distance of each individual from group means, indicated a low number of allocation errors in the species assignation (3.1% of northern individuals were placed in the southern group and 5.5% of the southern individuals were placed within the northern group; Table 2).

Table 2. – Classification matrix showing the cross-validated classification of each *Ensis* species.

Species	*E. loboi* n. sp.	*E. macha*	Total	Correct percentage
E. loboi n. sp.	93	3	96	96.9
E. macha	15	259	274	94.5

Taxonomy

After the molecular data published by Márquez et al. (2020) and the GM results presented in this study, two species of *Ensis* distributed along the Pacific coast of South America are now recognized. They are *Ensis loboi n. sp.*, distributed from Tubul, Chile (37°S) to Trujillo, Peru (8°S); and the Magellan *E. macha*, with a distribution range from San Matías Gulf (41°S) in the Atlantic Ocean to Niebla (40°S) in the Pacific Ocean. All records of *E. macha* mentioned northward of Tubul, Chile, must be considered synonyms of *E. loboi* (Soot-Ryen 1959, Peña 1971, Basly-Santa Maria 1983, Guzmán et al. 1998, Ramírez et al. 2003, Uribe et al. 2013, Paredes et al. 2016).

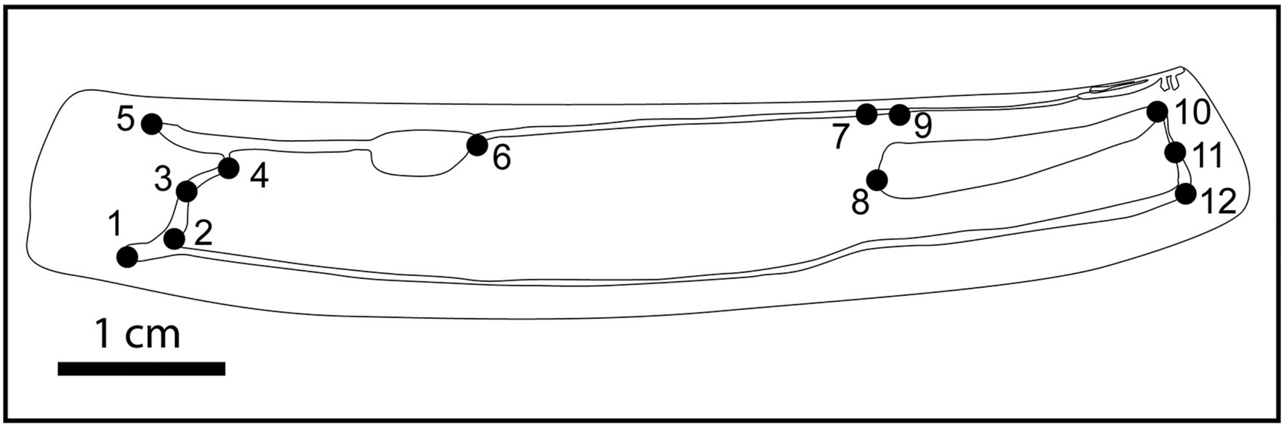

Fig. 2. – Position of the 12 landmarks on the inner surface of the left valve used to test the shape variation in *Ensis loboi* n. sp. and *E. macha*. The landmarks are postero-dorsal mantle projection (1), dorsal limit of pallial sinus (2), middle limit of pallial sinus (3), ventral limit of pallial sinus (4), postero-ventral mantle projection (5), posterior adductor muscle scar (6), horizontally oriented cardinal teeth (7, 9), internal end of anterior adductor muscle (8), antero-ventral mantle projection (10); middle point of anterior pallial line (11) and antero-dorsal mantle projection (12).

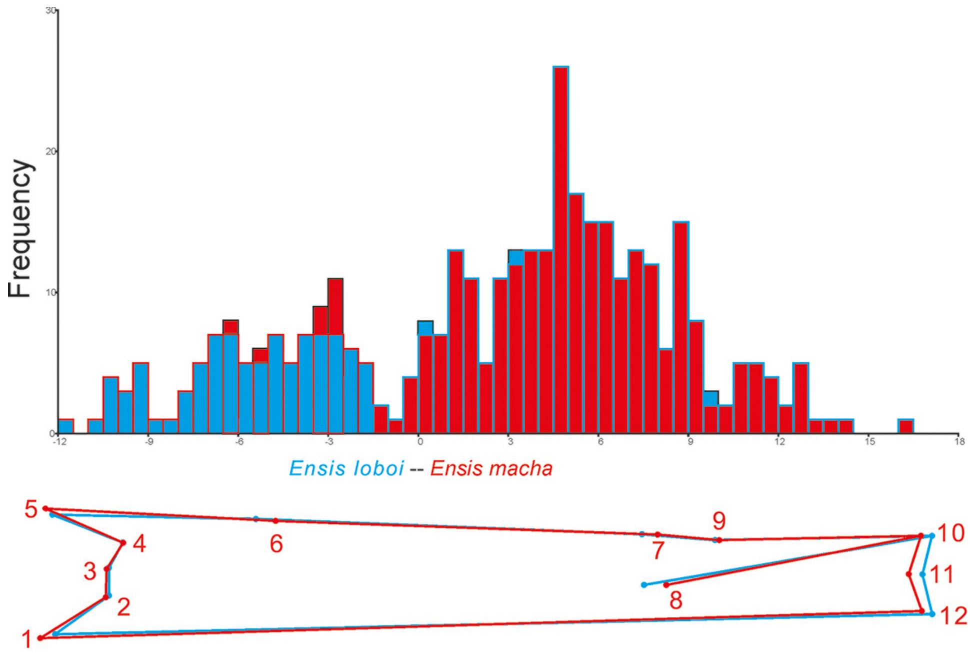

Fig. 3. – Discriminant analysis on inner shell shape of the *Ensis* southernmost species. The classification of discriminant frequencies predicted by the iterative cross-classification analysis between *E. loboi* n. sp. (cyan bars and wireframe graph) and *E. macha* (red bars and wireframe graph) are shown.

Family Pharidae H. Adams and A. Adams, 1856
Genus *Ensis* Schumacher, 1817

[= *Ensatella* Swainson, 1840: 365. Type species *Ensatella europaea* Swainson, 1840 (=*Ensis ensis* (Linnaeus, 1758), OD); *Hypogaea* Poli, 1791 (in Poli, 1791-1795): 29 (in part), name given for soft parts of species included in Solenoidea, Tellinidae and Pholadidae].

Type species: Ensis magnus Schumacher, 1817 by monotypy.

Distribution. Widely distributed along the Pacific coast of South America (Osorio and Reid 2002), southwestern USA to western Central America (Coan and Valentich-Scott 2012, Valentich-Scott et al. 2020), western Atlantic coast of South America (Rios 2009, Scarabino et al. 2016, Giacomino and Signorelli 2021), east coast of North America (Mikkelsen and Bieler 2007), Europe (Costello et al. 2001, Cosel 2009) and tropical west Africa (Cosel 2009).

Remarks. The genus *Ensis* includes 14 extant species (Cosel 2009, Coan and Valentich-Scott 2012, Valentich-Scott et al. 2020) widely distributed along both coasts of America, Europe and Western Africa. *Ensis loboi* n. sp. constitutes the fifteenth species of the genus.

Ensis loboi n. sp.
(Fig. 4A-R)

Ensis californicus of authors (not Dall, 1899) Alamo-Vázquez and Valdivieso-Milla, 1997: 141-142, 144, fig. 378.
Ensis macha of authors (not Molina, 1782) Stempell, 1899: 239-240 (in part); Soot-Ryen, 1959: 67; Peña, 1971: 137; Basly-Santa Maria, 1983: 26, pl. 10, fig. 83; Guzmán et al. 1998: 70-71; Ramírez et al. 2003: 268; Uribe et al. 2013: 230; Paredes et al. 2016: 149.

Type material: CNP-Inv 875, holotype. Paratypes: CNP-Inv 844, 1 specimen, CNP-Inv 872, 1 left valve, CNP-Inv 874, 1 specimen, Tubul, Talcahuano, Concepción, Chile (36.726202°S 73.132905°W).
Type locality. Tubul, Talcahuano, Concepción, Chile (36.726202°S 73.132905°W).

Etymology. This species is dedicated to José María “Lobo” Orensanz in recognition of his significant contribution to the field of fisheries and his invaluable advice to the authors of this manuscript over several years.

Description. Shell (Fig. 4A-R): large, thick, length up to 230 mm, cylindrical in cross section, elongate; dorsal and ventral margins almost straight, posterior end truncate; anterior end rounded; yellowish to dark brown periostracum, thin to moderately thick, partially eroded along the dorsal slope in larger specimens; exterior surface smooth with three sculptured zones, usually observed within *Ensis*; external ligament long and brown, over the dorsal edge, anteriorly placed behind the beaks; interior surface white to purple; hinge plate with two cardinal teeth in the right valve, one anterior and vertically oriented and one posterior and horizontally oriented; four cardinal teeth in the left valve, two vertically placed and two horizontally oriented, parallel to dorsal margin (Fig. 4), the horizontally oriented teeth are four times longer than the vertically oriented ones; ligament dark, opisthodetic (Fig. 4).

Additional material examined. Peru: CNP-Inv 3903, three specimens collected at Trujillo by José M. Lobo Orensanz. Chile: Bahía Coliumo, Dichato, Concepción (36.720555°S 73.150833°W), CNP-Inv 292, 19 valves, Tubul, Talcahuano, Concepción (36.726202°S 73.132905°W), Cnp-Inv-281, 26 specimens.

Fig. 4. – Type material of *Ensis loboi* n. sp. A-D: holotype, CNP-Inv 875. E-J: paratypes, CNP-Inv 281. K-N: paratypes CNP-Inv 844. O-R: paratypes, CNP-Inv 874. Scale bar 5-8, 11-14=2 cm; 9-10=5 mm; 15-22=3 cm.

Table 3. – Morphological differences between *Ensis macha* and *Ensis loboi* n. sp.

	Ensis loboi n. sp.	*Ensis macha*
Shell	Stronger and thicker	Thinner
Dorsal margin	Straight	Slightly concave
Distance between the posterior adductor muscle and the postero-ventral mantle projection (landmarks 5-6)	Shorter	Longer
Distance between ventral and dorsal mantle projections (landmarks 1-5)	More closed	More opened
Length of anterior adductor muscle (landmarks 10-8)	Longer	Shorter
External ligament	Longer	Slightly Shorter

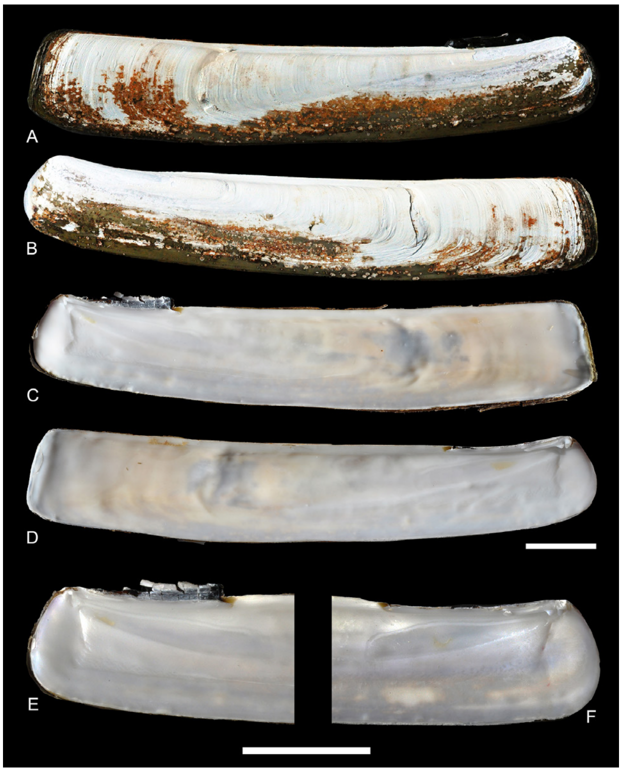

Fig. 5. – Specimens of *Ensis macha* for comparison. A-B, external view; C-D, internal view; E-F, detail of hinge plate. Scale bar = 2 cm.

Distribution. From Trujillo, Peru (8°8'S 79°3'W) to Tubul, Chile (37°13'S 73°26'W).

Habitat. E. macha and *E. loboi* inhabit superficial sandy bottoms, from the shallow subtidal to about 30 m depth, forming fishing grounds or banks (Osorio and Bahamonde 1970, Márquez and Van der Molen 2011). Razor clams can be found in a substrate characterized by a mixture of grain sizes, where fine and very fine sand with a low level of organic matter generally predominate (Aracena et al. 1998, Jaramillo 1998, Márquez and Van der Molen 2011).

Remarks. None of the synonyms of *E. macha* mentioned by Giacomino and Signorelli (2021) apply to the northern clade. *Solen poirieri* Mabille and Rochebrune, 1889 and *Solen scalprum* P. P. King, 1832 were described from the Magellan region. The registered type locality of *Ensis luzonicus* Dunker, 1862 (Luzon Island, Philippines) was erroneous. And the type of *Solen gladiolus*, described from "S. America", has not been found in the NHMUK. The synonymy with *E. macha* is currently open awaiting further analysis (Giacomino and Signorelli 2021). For these reasons, a new name is proposed for the northern clade. The shell morphology of *E. loboi* n. sp. and *E. macha* (Fig. 5) is similar. Slight differences are illustrated in Figure 6 and listed in Table 3. *Ensis loboi* n. sp. was found to possess a stronger and thicker shell than *E. macha.* In addition, the GM revealed slight differences between the two species. The main shape differences were the distance between the posterior adductor muscle and the postero-ventral mantle projection (landmarks 5-6, Fig. 3); the distance between ventral and dorsal mantle projections (landmarks 1-5, Fig. 3); and the length of the anterior adductor muscle (landmarks 10-8, Fig. 3). *Ensis californicus* was reported from southern Peru (Alamo-Vázquez and Valdivieso-Milla 1997: 141-142, 144, fig. 378). However, the illustrated specimen clearly differs from the type material of Dall (USNM 158891), which has a well-defined concave dorsal margin. This was also noticed by Valentich-Scott et al. (2020). In addition, the distribution of *E. californicus* is well documented from Sonora to Jalisco, Mexico (Coan and Valentich-Scott 2012). After the analysis of new material from Trujillo, Peru, the

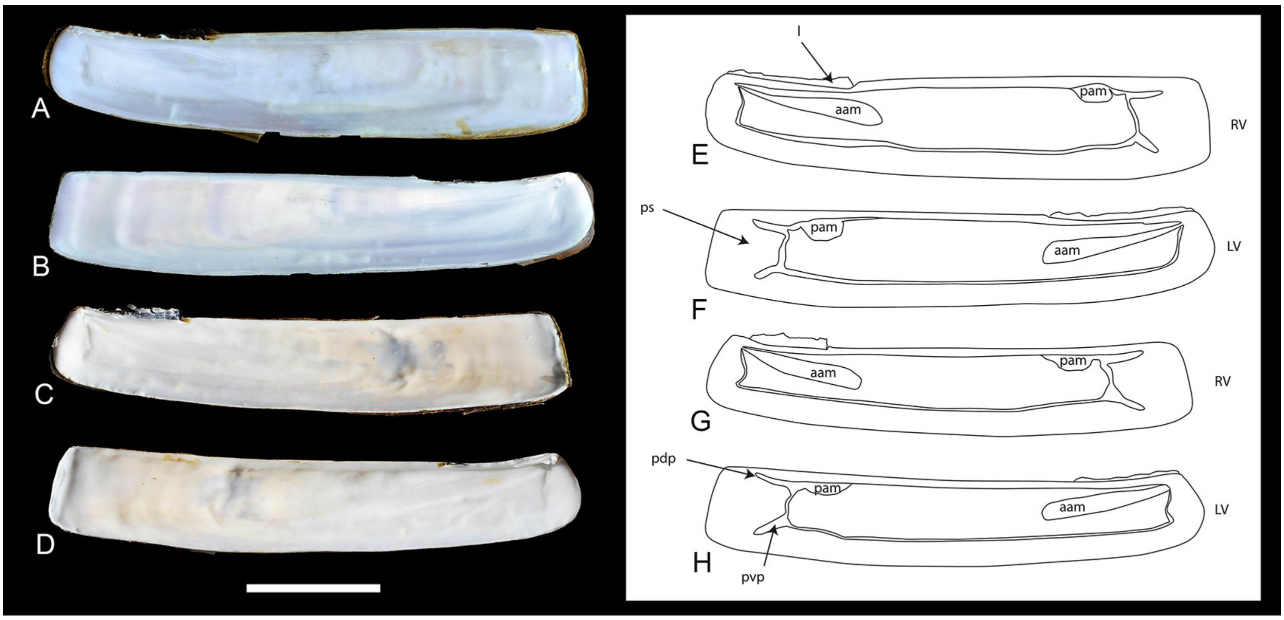

Fig. 6. – Morphological comparison between *Ensis loboi* n. sp. and *E. macha*. A-B, E-F: *E. loboi* n. sp. C-D, G-H: *E. macha*. Scale bar = 4 cm.

specimens illustrated by Alamo-Vázquez and Valdivieso-Milla (1997) must be considered *E. loboi* n. sp.

DISCUSSION

Morphological studies and GM were used to distinguish *Ensis loboi* n. sp. (the northern clade) from *E. macha* (the southern clade). Specimens collected from Chiloé Island, Chile (42°35'S) were described by Molina (1782) as *Solen macha*. Thus, the southern clade must retain the name *E. macha* and the northern clade must be considered as *E. loboi* n. sp. Additionally, slight shell shape components allowed both species of *Ensis* to be delineated with high resolution using GM based on 2D landmark configuration. These two clades were recently revealed by Márquez et al. (2020) on the basis of mitochondrial and nuclear loci. The genetic distance of COI sequence data between the two clades was similar to the magnitude of divergence between other recognized species of *Ensis* (Vierna et al. 2012, Vierna 2014) and was greater than the sequence divergence expected for more than 98% of 13320 species pairs across the animal kingdom (2%, Hebert et al. 2003). In addition, the nuclear genetic divergences were similar to those found for different species by previous studies using multiple markers (e.g. Klimov et al. 2019). Morphological and GM analysis reached the same conclusion as that obtained from genetic data reported by Márquez et al. (2020). Many authors have reported genetic differentiation for species distributed along the southeastern Pacific coast. In the case of *E. macha* and *E. loboi* n. sp., the biogeographic break was observed at 36-39°S (Márquez et al. 2020). This result coincides with those reported for other taxa (Fraser et al. 2009, Montecinos et al. 2012; Trovant et al. 2015). The presence of genetic structure was found to characterize several taxa across central and northern Chile and Peru (Hewitt 1996). The opposite pattern was observed in several species distributed along the Magellan province (de Aranzamendi et al. 2011, Ceballos et al. 2012, Trovant et al. 2015). However, no signs of genetic structure were found in the northern clade (*E. loboi* n. sp.) by Márquez et al. (2020). This result could be related to the fact that only two populations were sampled. Additional localities in northern Chile and Peru will help to highlight the evolutionary history of *E. loboi* n. sp. A potential scenario to explain the observed findings is that the differentiation between the northern and southern clades may have been initiated during the late Pleistocene. Glacial activity affects the Pacific Ocean south of 39°S, reaching the Atlantic Ocean in southernmost Patagonia and Tierra del Fuego (Clapperton 1993, Sugden et al. 2005), and could have separated the populations of northern Central Chile and Peru from those of southern Argentina. The isolation of populations could have interrupted gene flow and over time, resulted in the concomitant genetic differentiation observed between these two populations.

Several studies have demonstrated overexploitation of populations of *E. macha* along the coasts of Peru and southeastern Chile (Espinoza et al. 2010, Hernández et al. 2011). The management of a species depends on a solid, well-founded science-based taxonomy and systematics (Mace 2004). The South American *Ensis* fishery is managed as one species throughout its distribution. However, this study suggests cryptic diversity in *Ensis macha*. Overlooking a second *Ensis* species may have contributed to the overestimation of the population size, resulting in overfishing. The finding of a new species of *Ensis* is highly relevant for managing and conserving this important fishing resource in South America.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

ETHICAL APPROVAL

All applicable international, national and/or institutional guidelines for the care and use of animals were followed by the authors.

SAMPLING AND FIELD STUDIES

All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities. The study is compliant with the CBD and Nagoya protocols.

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