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Resolving the conflictive phylogenetic relationships of *Oceanites* (Oceanitidae: Procellariiformes) with the description of a new species

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Abstract

The family Oceanitidae, formerly considered a subfamily of Hydrobatidae, includes all the small storm-petrels of the southern hemisphere. The ancestor-descendent relationships and evolutionary history of one of its genera, *Oceanites*, have been partially studied, yielding contrasting results. We revised the phylogenetic relationships of this group using Bayesian inference (BI) based on new sequence data of the mitochondrial gene Cytb and linear morphological measurements of all species and five subspecies-level taxa in *Oceanites*, including a new taxon from the Chilean Andes. Our BI results show that the *Oceanites* genus is monophyletic and composed of four well-supported clades (posterior probability > 0.95): (1) *chilensis*; (2) *exasperatus*; (3) *gracilis*, *pincoyae,* and *barrosi* **sp. nov.**; and (4) *oceanicus* and *galapagoensis*. The species *O. chilensis* is a basal clade within *Oceanites*. According to our time-calibrated tree, the split between *Oceanites* and the other genera in Family Oceanitidae is estimated to be ~35.9 Mya, and the oldest divergence within *Oceanites* (the split between *O. chilensis* and other *Oceanites*) was dated to the early Miocene, around c. 21.3 Mya. The most probable geographic origin of *Oceanites* is the Southern Ocean. The morphological data suggest continuous size variation between *Oceanites* taxa, ranging from smallest in *gracilis* to largest in *exasperatus*. Based on our phylogenetic hypothesis, and morphological analyses, we suggest elevating to species status the taxa *galapagoensis*, *chilensis,* and *exasperatus*, and we describe a new taxon *barrosi* **sp. nov**., thus recognizing a total of seven species within the genus *Oceanites*.

Key words: Evolution, storm-petrels, systematics, taxonomy

Introduction

The family Oceanitidae is comprised of storm-petrels that have their phylogeographic origin in the Southern Hemisphere (Onley & Scofield 2007), including 10 species among the genera *Oceanites*, *Garrodia*, *Pelagodroma*, *Fregetta*, and *Nesofregetta* (Clements *et al*. 2023). The at-sea distribution of this family includes tropical, temperate, subantarctic, and Antarctic seas in the Southern Hemisphere, including temperate waters of the North Atlantic (Winkler *et al.* 2020). This family was formerly considered a subfamily within Hydrobatidae (Sibley *et al.* 1990; Nunn & Stanley 1998), even though Forbes (1882) long ago had suggested, based on osteological and myological analyses, that the species within Oceanitidae do not group with other storm-petrels. More recently, molecular

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phylogenetic studies confirmed that Oceanitidae is not a sister clade to Hydrobatidae (Kennedy & Page 2002; Hackett *et al.* 2008; Prum *et al.* 2015; Reddy *et al.* 2017). However, systematics within Oceanitidae remain unclear, especially within the genus *Oceanites* (Howell & Schmitt 2016). Currently, it is accepted that the genus *Oceanites* comprises three species (*sensu* Clements *et al.* 2023): *O. oceanicus* (Kuhl, 1820); *O. gracilis* (Elliot, 1859)*;* and *O. pincoyae* Harrison *et al.*, 2013; but the taxonomic status of subspecies (and some species) continues to be controversial (see Fig. 1).

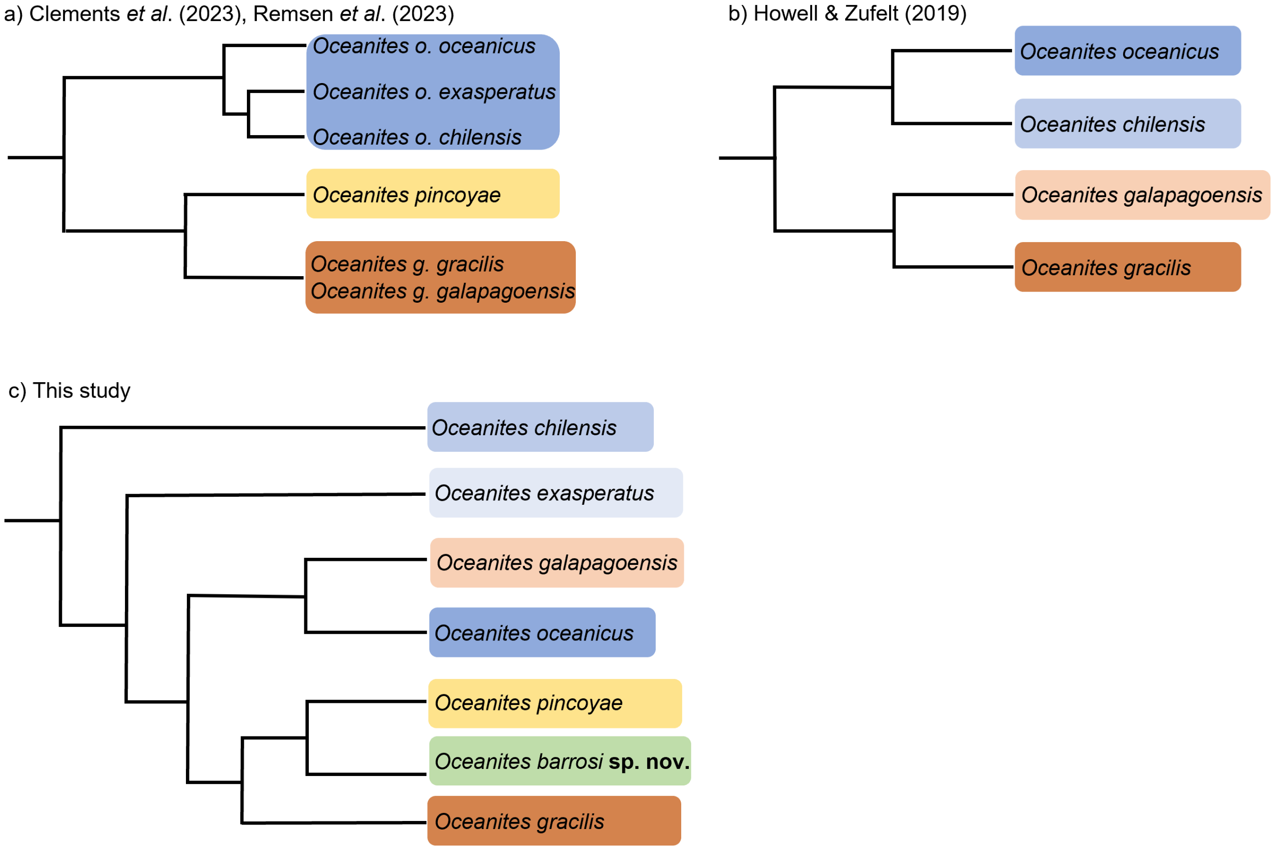

FIGURE 1. Phylogenetic hypotheses of the genus *Oceanites* in previous treatments compared with this work. a) Morphological classification suggested by Clements *et al.* (2023) and Remsen *et al.* (2023). Remsen *et al.* (2023) only consider species, not subspecies. b) Morphological classification suggested by Howell & Zufelt (2019). c) Bayesian phylogenetic hypothesis of *Oceanites* genus presented in the results of this study, based on the maximum credibility tree estimated from Cytb sequences. Colors represent the similarities between taxonomic proposals.

The species *O. oceanicus sensu lato* is considered to comprise three subspecies (Clements *et al.* 2023): nominate *O. o. oceanicus* (Kuhl, 1820); *O. o. exasperatus* Mathews, 1912*;* and *O. o. chilensis* Mathews, 1934. The species *O. gracilis sensu lato* has two subspecies, nominate *O. g. gracilis* (Elliot, 1859) and *O. g. galapagoensis* Lowe, 1921, while *O. pincoyae* is a recently described monotypic species (Harrison *et al.* 2013; Remsen *et al.* 2023). However, based on their field observations, Howell & Zufelt (2019) suggest that there are four species-level taxa within *Oceanites*: Wilson's Storm-Petrel *O. oceanicus* of Antarctica and subantarctic islands; Fuegian Storm-Petrel *O. chilensis* of central and southern Chile and Argentina (and probably Falklands/Malvinas); Elliot's Storm-Petrel *O. gracilis* of Peru and northern Chile; and Lowe's Storm-Petrel *O. galapagoensis*, of the Galapagos (Fig. 1). However, these authors suggest that the species status of Pincoya Storm-Petrel *O. pincoyae* still requires elucidation (Howell & Schmitt 2016; Howell & Zufelt 2019).

Previous studies of the systematics of the genus only included a partial representation of *Oceanites*. The first phylogeny of Procellariiformes based on mitochondrial DNA Cytb (Nunn & Stanley 1998) considered Oceanitidae as a subfamily of Hydrobatidae despite the evident paraphyly of these clades. This study only included samples of *O. oceanicus* (no subspecies is identified), which is shown as a sister species of a clade that includes *Pelagodroma marina* (Latham, 1790), *Garrodia nereis* (Gould, 1841), *Fregetta tropica* (Gould, 1844)*,* and *F. grallaria* (Vieillot, 1818). Later, Robertson *et al.* (2011) incorporated a sequence of *O. o. exasperatus* into a new phylogeny of Oceanitidae, which showed a close relationship with *O. oceanicus* based on Cytb (Nunn & Stanley 1998), and in a phylogeny based on the 7th intron of b-fibrinogen, *O. o. exasperatus* was sister to a clade that includes *Fregetta* and *Pelagodroma* (see Robertson *et al.* 2011). Robertson *et al.* (2011) also generated *O. g. gracilis* and *O. g. galapagoensis* sequences, but due to their short sequences (i.e., 132 bp) these were not included in the phylogeny. Other studies have only shown the relationships of *O. oceanicus* (based on Cytb) with the other species of the family (e.g., Hackett *et al.* 2008; Cibois *et al.* 2015; Prum *et al.* 2015; Robertson *et al.* 2016; Reddy *et al.* 2017) or used *O. gracilis* (based on ND1) as an outgroup of a phylogeny of the evolution of *Oceanodroma* (Sausner *et al.* 2016).

Given the disjunctions in the breeding range between taxa of the *Oceanites oceanicus* complex and that these have been historically exposed to fluctuating and contrasting historical and geological events, the occurrence of geographically structured, deeply diverged lineages is expected. The foregoing, added to signs of phenotypic and genetic variation, make this complex a good candidate for species delimitation studies to evaluate the hypothesis of sibling or cryptic species and the monophyly of the clades. Therefore, using geographically diverse sampling based on genetic and morphological information, the main goal of this work is to evaluate species limits in the *O. oceanicus* complex under the hypothesis that the *O. oceanicus* complex corresponds to more than one species forming monophyletic clades.

Material and methods

Sampling

We sampled individuals from *O. g. gracilis* (N = 4), *O. g. galapagoensis* (N = 2), *O. o. chilensis* (N = 10), and *O. pincoyae* (N = 1) from several localities in northern and southern Chile and Ecuador (Fig. S1; Table 1). Birds were captured in the field using mist-nets, and each individual was measured and photographed. For genetic analysis, we collected blood samples by venipuncture of the brachial vein for *O. g. gracilis*, *O. g. galapagoensis,* and *O. o. chilensis*. After blood sampling, individuals were returned to their habitat. All captures in Chile were under permits No. 5022/2014, 5742/2016, and 9853/2019 from the Servicio Agrícola Ganadero (SAG). All captures in the Galapagos were conducted under research permit PC-26-14 issued by the Ecuador Department of the Environment and Galapagos National Park, with the exportation of samples and specimens from Ecuador through permit 185-2014 DPNG. Genetic samples from *O. g. galapagoensis*, *O. o. oceanicus*, and *O. o. exasperatus* were obtained from previous studies and GenBank (Table 1). For species of the genera *Garrodia*, *Pelagodroma*, *Fregetta*, and *Nesofregetta,* we used the sequences generated by Nunn & Stanley (1998) and Robertson *et al.* (2011) (Table 1). Considering the paraphyletic relationships between Hydrobatidae and Oceanitidae, we used as outgroups individuals from Hydrobatidae, Diomedeidae, and Procellariidae.

TABLE 1. Taxon sample list, including institution, tissue number, country, region and GenBank accession number per locus.

N°	Taxon	Institution	Tissue	Locality	Region	Cytb	Breeding area	Reference
1	*Oceanites exasperatus*	UNC Wilmington	NCSM 22701	Carteret	North Carolina	KJ400323	Antarctica	Torres *et al.* 2014
2	*Oceanites exasperatus*	University of Otago	B15	-	-	JN587565	Antarctica	Robertson *et al.* 2011
3	*Oceanites exasperatus*	American Museum of Natural History	WILSON-1	-	-	AF076062	Antarctica	Nunn and Stanley 1998
4	*Oceanites exasperatus*	-	-	Livingston Island	Antarctica	KU217327	Antarctica	Wallace *et al.* 2017

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TABLE 1. (Continued)

N°	Taxon	Institution	Tissue	Locality	Region	Cytb	Breeding area	Reference
5	*Oceanites exasperatus*	Wildlife Institute of India	Carcass	Groves Peninsula	Antarctica	MN642063-MN642071, MN642076-MN642078, MW679035-MW679038	Antarctica	Pacha *et al.* 2023
6	*Oceanites exasperatus*	Wildlife Institute of India	Carcass	Easther Island	Antarctica	MN642072, MN642079	Antarctica	Pacha *et al.* 2023
7	*Oceanites exasperatus*	Wildlife Institute of India	Carcass	Fishers Island	Antarctica	MN642073	Antarctica	Pacha *et al.* 2023
8	*Oceanites exasperatus*	Wildlife Institute of India	Carcass	Broknes Peninsula	Antarctica	MN642074, MN642075	Antarctica	Pacha *et al.* 2023
9	*Oceanites exasperatus*	Wildlife Institute of India	Carcass	Stornes Island	Antarctica	MW679039	Antarctica	Pacha *et al.* 2023
10	*Oceanites exasperatus*	Wildlife Institute of India	Carcass	Bølingen	Antarctica	MW679040	Antarctica	Pacha *et al.* 2023
11	*Oceanites oceanicus*	Justus Liebig University Giessen	Blood	Isla Beauchene	Falklands/ Malvinas	KP122196	Falklands_SG	Moodley *et al.* 2015
12	*Oceanites oceanicus*	Justus Liebig University Giessen	Blood	Isla Beauchene	Falklands/ Malvinas	KP122195	Falklands_SG	Moodley *et al.* 2015
13	*Oceanites oceanicus*	Justus Liebig University Giessen	Blood	Isla Beauchene	Falklands/ Malvinas	KP122194	Falklands_SG	Moodley *et al.* 2015
14	*Oceanites oceanicus*	Justus Liebig University Giessen	Blood	Isla Beauchene	Falklands/ Malvinas	KP122193	Falklands_SG	Moodley *et al.* 2015
15	*Oceanites oceanicus*	Justus Liebig University Giessen	Blood	Isla Beauchene	Falklands/ Malvinas	KM050770	Falklands_SG	Moodley *et al.* 2015
16	*Oceanites barrosi* **sp. nov.**	MZUC-UCCC	OCC01	El Morado	Metropolitana	PP480632	Chile	This study
17	*Oceanites barrosi* **sp. nov.**	MZUC-UCCC	OCC02	Río Colorado	Metropolitana	PP480633	Chile	This study
18	*Oceanites barrosi* **sp. nov.**	MZUC-UCCC	OCC03	Río Colorado	Metropolitana	PP480634	Chile	This study
19	*Oceanites chilensis*	Blood	OC14	Punta Arenas	Magallanes	PP480640	Chile	This study
20	*Oceanites chilensis*	Blood	OC15	Punta Arenas	Magallanes	PP480641	Chile	This study
21	*Oceanites pincoyae*	Feather sample	OP01	Aysén	Aysén	PP480635	Chile	This study
22	*Oceanites gracilis*	Blood	OG01	Arica	Arica y Parinacota	PP480636	Chile	This study
23	*Oceanites gracilis*	Blood	OG03	Isla Chungungo	Coquimbo	PP480637	Chile	This study
24	*Oceanites gracilis*	Blood	OG05	Isla Chungungo	Coquimbo	PP480638	Chile	This study
25	*Oceanites gracilis*	Blood	OG06	Isla Chungungo	Coquimbo	PP480639	Chile	This study

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TABLE 1. (Continued)

N°	Taxon	Institution	Tissue	Locality	Region	Cytb	Breeding area	Reference
26	*Oceanites gracilis*	University of Otago	CMNZ AV20792	Pacific Ocean?	Pacific Ocean?	JN587554	Perú	Robertson *et al.* 2011
27	*Oceanites galapagoensis*	University of Otago	Blood GP01	Galapagos	Ecuador	OR130459	Ecuador	This study
28	*Oceanites galapagoensis*	University of Otago	Blood SB12	Galapagos	Ecuador	OR130460	Ecuador	This study

DNA extraction, amplification, and sequencing

Genomic DNA was extracted from samples following the protocol of Fetzner (1999) and using the QIAGEN DNeasy kit. We sequenced the mitochondrial gene cytochrome b (Cytb) using the primer sequences L14863-forward: TTT-GCC-CTA-TCT-ATC-CTC-AT and b6-reverse: GTC-TTC-AGT-TTT-TGG-TTT-ACA-AGA-C following the protocol described in Sorenson *et al.* (1999). Thermal cycling was performed using the GeneAmp® PCR System 2700 (Applied Biosystems) under the following conditions: 2 min at 94 °C, 30 cycles at 94 °C for 45 s, 30 cycles at 45 °C for 45 s, and 30 cycles at 72 °C for 1 min, with a final extension at 72 °C for 5 min (*sensu* Techow *et al.* 2009). PCR products were sequenced in both directions through automatic sequencing using the equipment ABI3730XL of Macrogen (Korea). Sequences were edited using Codon Code Aligner v. 3.0.3 (Codon Code Corporation, 2007) and translated into amino acids to corroborate the absence of stop codons. Sequence alignment was conducted in MUSCLE with 100 iterations (Edgar 2004), producing a final alignment length of 1,072 bp for 40 samples. To avoid obtaining spurious outcomes resulting from the lost phylogenetic information due to substitution saturation, we tested whether the sequences were useful for phylogenetic analysis through Xia's test (Xia *et al.* 2003) implemented in DAMBE v7 (Xia 2018). Xia's test is an entropy-based index that estimates a substitution saturation index (Iss) and compares the Iss to a critical substitution saturation index (Iss.c) via a randomization process with 95% confidence intervals; the proportion of invariable sites for this analysis was determined in jModeltest 2 (Darriba *et al.* 2012). All sequences have been deposited in GenBank (Table 1).

Phylogenetic analyses

We used Bayesian inference (BI) approaches for phylogenetic reconstruction using the BEAST v. 1.10.4 program (Drummond *et al.* 2012), with the 'Yule speciation model' for the tree prior. We identified the best-fit nucleotide substitution model using jModeltest 2 (Darriba *et al*. 2012), which indicated HKY + Γ as the best-fit model for Cytb. We ran all analyses for 100 million generations, and we sampled every 1,000 steps; the first 25% of the data was discarded as burn-in. The convergence of MCMC analysis was examined visually in Tracer v1.6 (Rambaut & Drummond 2009). We also recovered a time-calibrated tree using the BEAST v. 1.10.4 program with the same substitution model described above. We compared four molecular clock models: the strict clock, the lognormal relaxed clock, the exponential relaxed clock, and the random local clock, determining the best fit by a Bayes Factor analysis. We chose the lognormal relaxed clock model because it returned a score of 20 log-likelihood units greater than the other models. We used a 'Yule speciation process' for the trees and ran the analysis for 100 million generations, sampling every 1,000, specifying a burn-in of 25%, and analyzing the posterior output in TRACER v. 1.6 achieving ESS values >200 for all parameter values. We estimated dates with a divergence rate of 0.92% per Myr for Cytb following the findings of Nunn & Stanley (1998) that MTCYB evolution was slower in procellariforms than in most other birds and correlated with body size. Finally, we calculated uncorrected pairwise genetic distances between taxa based on Cytb in MEGA11 (Tamura *et al.* 2021).

Model-based biogeographic analysis

To reconstruct the biogeographic process that promoted speciation of the genus, we used different biogeographical models in the package BioGeoBears (Matzke 2012) implemented in R v.3.4.0. We started with the DEC model (Ree

& Smith, 2008) with two free parameters: "d" (dispersal rate) and "e" (extinction rate) and a fixed cladogenetic model (cladogenetic event allowed: vicariance, sympatric-subset speciation and sympatric range-copying). We then implemented the dispersal-vicariance-like (DIVALIKE; Ronquist 1997) and Bayesian analysis of biogeography when the number of areas is large (BAYAREALIKE; Landis *et al*. 2013) models in the BioGeoBears. BioGeoBears optimizes ancestral range states onto internal nodes of a tree and produces likelihood estimates of the transitions between states on these nodes. The DIVALIKE model functions in a similar likelihood framework as the dispersal-extinction-cladogenesis model (Ree & Smith 2008) but excludes certain biogeographic scenarios including subset sympatry. BAYAREALIKE, in contrast, only allows for events to happen along branches and not at cladogenesis events. We constructed a geographic range matrix (adapted from Cracraft 1985), coding each taxon as present or absent in one or multiple areas. We included the following geographic regions in the model, based on the marine biogeographic realm classification of Costello *et al.* (2017): A) The Southeast Pacific; B) The Southern Ocean (including Antarctica); and C) The Atlantic. Varying the maximum number of areas a taxon can occupy (i.e. 2–3 areas) had little effect on likelihood estimates. We finally compared three main models, including and excluding the founder-event speciation parameter J, where the new species "jumps" to a range outside of the ancestral range, resulting in a total of six models (i.e., DEC, DEC+J, DIVALIKE, DIVALIKE+J, BAYAREALIKE, and BAYAREALIKE+J). The model selection was based on the Akaike information criterion adjusted for small samples (AICc) and their relative weights (AICcw; Burnham & Anderson 2002).

Morphological and statistical analysis

To evaluate morphological differences between the six currently recognized taxa of *Oceanites*, we created a database with morphological information from individuals caught in mist-nets (new taxon N = 12, *O. gracilis gracilis* N = 5, *O. gracilis galapagoensis* N = 18, and *O. oceanicus chilensis* N = 2) and museum specimens (USA: AMNH and NMNH; Chile: MNHN and MZUC-CCC) for a total of 79 individuals. Except for *O. pincoyae* measurements (N = 12; Harrison *et al*. 2013), all the information in the database is unpublished and was measured by H.V.N. and R.B. The database includes five measurements in mm: 1) natural wing length (measured from the curve of the wing to the tip of the longest primary feather); 2) length of tarsus; 3) length of exposed culmen or beak length; 4) mid-toe claw length (with nail); and 5) tail length along central rectrices.

Because some variables may not follow a normal distribution, we ran a Kolmogorov-Smirnov normality test to evaluate the distribution of the morphological database. Principal Component Analyses (PCA) were conducted to investigate whether species exhibit morphological differences, and which measurements explain these differences. A Kaiser-Meyer-Olkin (KMO) test was performed to determine the suitability of the data set for PCA (Budaev 2010). Higher KMO values indicate sampling adequacy for each model variable, with values >0.90 being ideal (Budaev 2010). Bartlett's test of sphericity was then performed to assess for an adequate amount of collinearity ($p < 0.05$) between variables (Pett *et al.* 2003). All PCA analyses were conducted in R (R Development Core Team 2013) using the *prcomp* function and *ggbiplot* package. We retained the two first PC axes that presented eigenvalues >0.8 for graphical display. In a complementary way, to evaluate differences between previously assigned taxa, we ran linear discriminant function analysis (LDA) to investigate the relationships between species. All LDA analyses were conducted in R using the MASS package (R Development Core Team 2013).

Results

Phylogenetic analysis

Sequences of 1,072 bp in length for the Cytb locus were obtained and the result of Xia's test suggests low saturation, as the critical index of substitution saturation value (Iss.c = 0.754) was significantly higher than the observed index of substitution saturation values (Iss = 0.562; $p < 0.0001$), therefore, the sequences were deemed suitable for performing phylogenetic analyses. The genus *Oceanites* was recovered as a monophyletic group strongly supported by a high posterior probability (PP = 1.0) (Fig. 2). Our trees revealed four major subclades: (1) *chilensis*; (2) *exasperatus*; (3) *gracilis*, *pincoyae*, and *barrosi* **sp. nov.**; and (4) *oceanicus* and *galapagoensis* (Fig. 2). This tree also shows that *gracilis*, *galapagoensis*, *oceanicus*, *chilensis*, *pincoyae,* and *exasperatus* are each monophyletic (Fig. 2). In addition, the populations of *Oceanites* present in central Chile (*barrosi* **sp. nov.**) represent a sister group with *O. pincoyae* but with high divergence (Fig. 2, Table 1). Several of the taxa presently considered polytypic species are shown to be paraphyletic in our tree (Figs 1 and 2). The taxon *O. chilensis* (formerly *O. oceanicus chilensis*) appears as a basal clade to the other *Oceanites* species (Fig. 2). Samples from the Andes of central Chile (formerly considered a population of *chilensis*), form a clade together with *pincoyae* and are phylogenetically distant from the samples of *chilensis* from their main distribution (close to *Terra Typica*; Fig. 2). The genetic distance between species varied from 4% to 19% (Table 2).

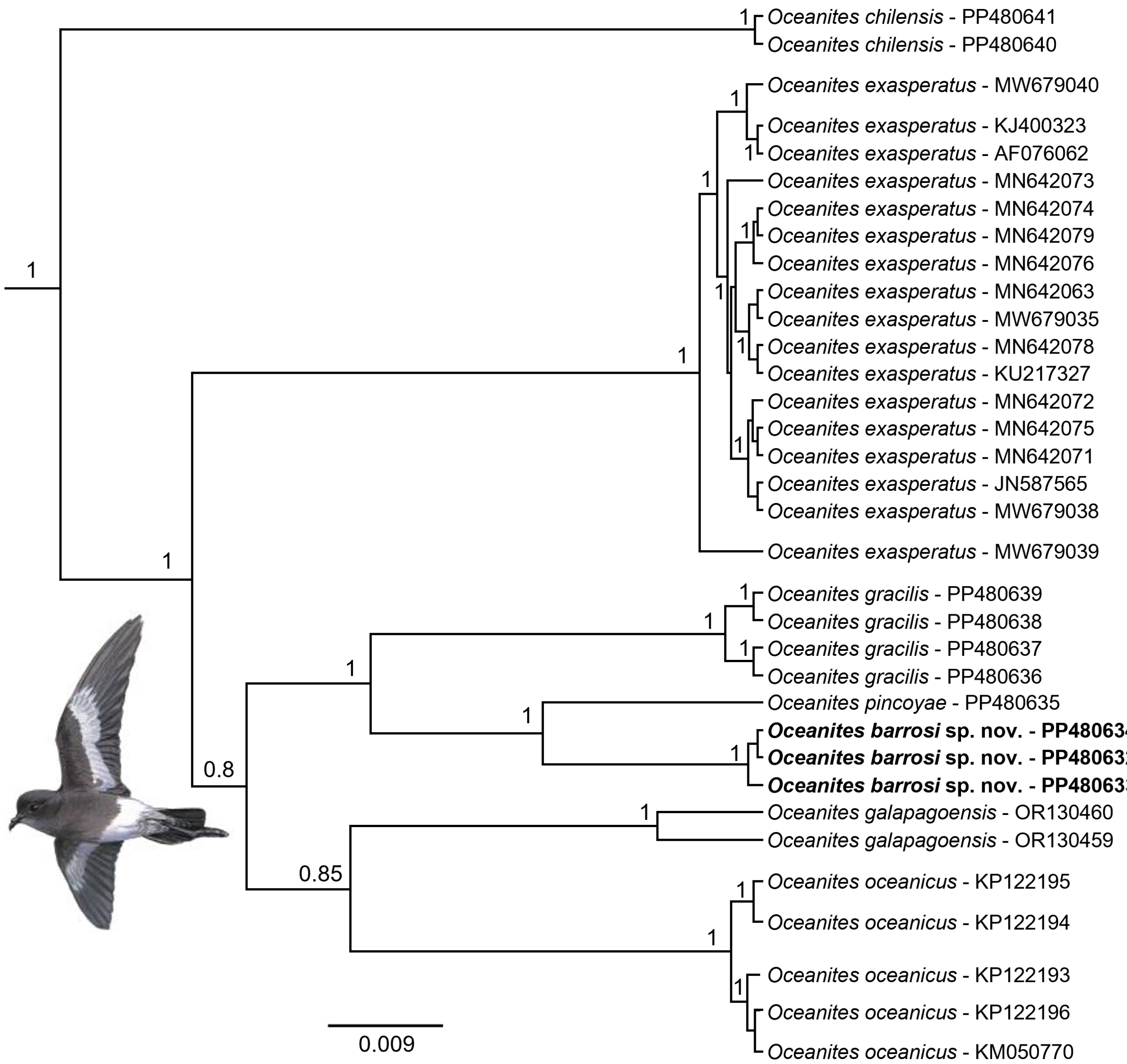

FIGURE 2. Phylogenetic hypothesis of the genus *Oceanites* based on BEAST from Cytb gene. Numbers on nodes are posterior probability values from the Bayesian analysis. Outgroups are not shown. Inset illustration *Oceanites pincoyae* from *Handbook of the Birds of the World*.

According to our time-calibrated tree (Fig. S2), the split between *Oceanites* genera and the other genera in Oceanitidae is estimated at ~32.7 Mya (40.7–22.4 Mya; 95% HPD), and the oldest divergence within *Oceanites* (the split between *O. chilensis* and other *Oceanites*) dated to the late Oligocene, around c. 21.3 Mya (29.3–13.3 Mya; 95% HPD). The most recent split was between *O. pincoyae* and *O. barrosi* **sp. nov.** dated to the Late Miocene, around c. 6.7 Mya (10.7–2.6 Mya; 95% HPD).

TABLE 2. Uncorrected pairwise genetic differences based on Cytb sequences of *Oceanites* species analyzed in MEGA11 (Tamura *et al.* 2021). This analysis involved the average values for each taxon. All ambiguous positions were removed for each sequence pair (pairwise deletion option). There was a total of 1,072 positions in the final dataset.

Species and ID	1	2	3	4	5	6	7
Oceanites pincoyae	-						
Oceanites gracilis	0.09	-					
Oceanites oceanicus	0.03	0.11	-				
Oceanites galapagoensis	0.09	0.11	0.04	-			
Oceanites exasperatus	0.05	0.13	0.04	0.05	-		
Oceanites chilensis	0.06	0.19	0.05	0.06	0.05	-	
Oceanites barrosi **sp. nov.**	0.05	0.09	0.03	0.08	0.04	0.07	-

Biogeographic analysis

The DIVALIKE+j model was supported as the most likely (Table 3), outperforming both BAYAREALIKE and DEC models to describe the origin of the biogeographic region assigned to the species distributions given the time-calibrated phylogeny. Jump dispersal (j) is important according to this model, with a relatively low role for dispersal and extinction. BioGeoBears allocates the oldest node in the *Oceanites* clade (basal node) with the highest likelihood of Southern Ocean origin (Fig. 3). From that area, jump-dispersal event colonization to the south-east Pacific occurred around 15 to 18 Mya, promoting the origin of *O. gracilis*, *O. pincoyae,* and *O. barrosi* **sp. nov.** Another colonization event around 15 Mya promoted the origin of *O. galapagoensis* and *O. oceanicus* in the Southern and Atlantic oceans (Fig. 3). The species *O. exasperatus* would have colonized Antarctica around 17 Mya.

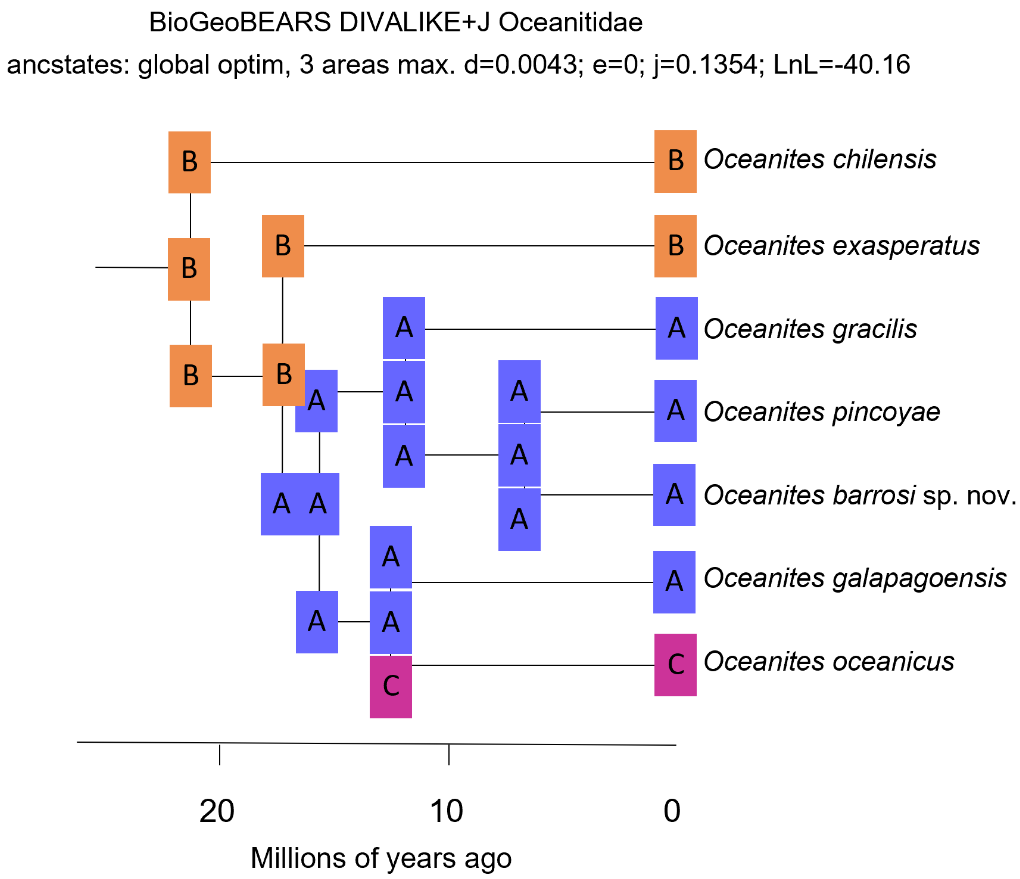

FIGURE 3. Biogeography and diversification of *Oceanites* genera plotted on consensus tree based on Cytb gene. Pie charts indicate ancestral range states at each node according to DIVALIKE+j model in BioGeoBears: A) South-east Pacific; B) Southern Ocean (including Antarctica); and C) Atlantic. Outgroups are not shown.

TABLE 3. Results of ancestral range estimation analyses from BioGeoBears, using no constraints on adjacency of four defined marine biogeographic realms classification, df is degrees of freedom per model, LnL is log likelihood, AICw is weight of Akaike information criterion, d is dispersal, e is extinction, and bold indicates the most likely model.

Model	LnL	numparams	d	e	j	AICc	AICc_wt
DEC	-40.56	3	0.0035	1.00E-12	0.15	88.04	0.29
DEC+J	-40.84	3	0.0041	1.00E-12	0.1	88.61	0.22
DIVALIKE	-46.57	2	0.01	1.00E-12	0	97.59	0.0025
DIVALIKE+J	**-40.16**	**3**	**0.0043**	**1.00E-12**	**0.14**	**87.25**	**0.44**
BAYAREALIKE	-61.95	2	0.0082	0.025	0	128.4	5.2E-10
BAYAREALIKE+J	-42.42	3	0.0029	1.00E-07	0.16	91.75	0.046

Morphological analysis

For the five measurements, the Bartlett's test of sphericity and KMO measures were p<0.001 and >0.78, respectively. PCs 1 and 2 presented the highest eigenvalues (>0.8) and explained 75.6% of the total variation (Fig. 4, Table S1). PC1 correlated positively with 'wing length', 'tail length', 'tarsus length', and 'mid-toe claw' and can be interpreted as a component reflecting overall size; PC2 correlated positively with 'culmen'. Scatterplots of PCs showed a gradual variation between *Oceanites* species in the PC1 axis, with only marked differences between *gracilis* and the *oceanicus* complex, and overlapping between *pincoyae*-*chilensis* and *oceanicus*-*exasperatus,* respectively (Fig. 4). PC2, or the culmen measures, do not allow for separation of the populations. The LDA based on PCA results resulted in a 77.3% correct classification of the assigned species. Only three individuals of *pincoyae* were assigned to *chilensis*, one individual of *chilensis* was assigned to *exasperatus,* and two individuals of *oceanicus* were assigned to *barrosi* and two others to *exasperatus*, respectively (Fig. S3, Table S2).

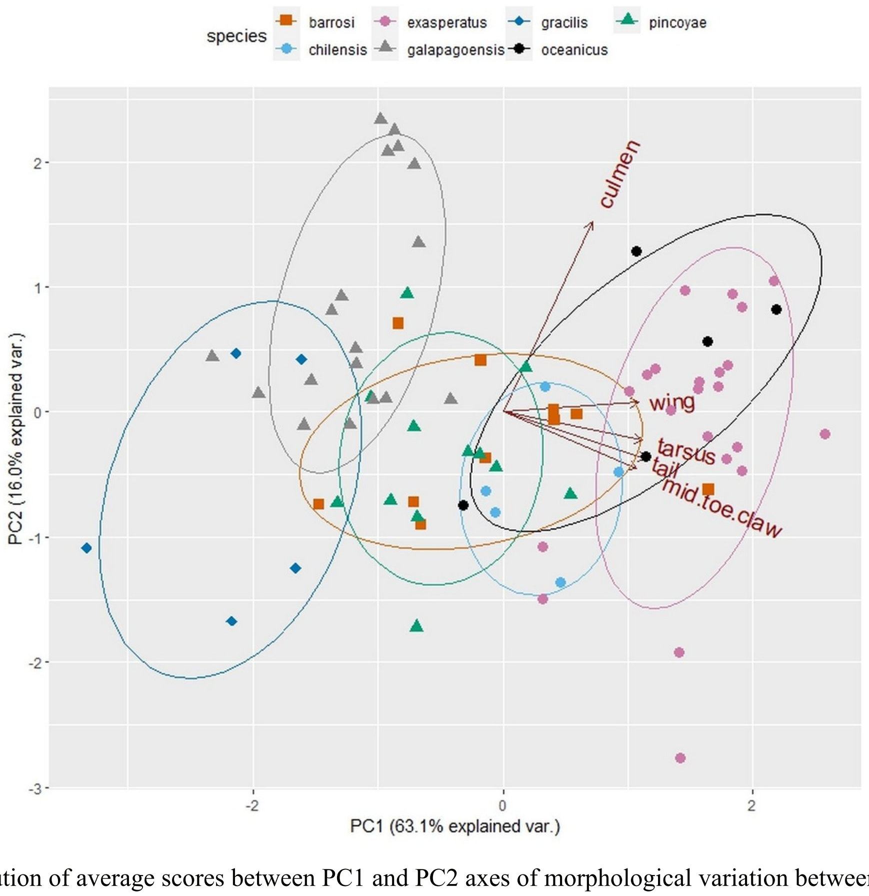

FIGURE 4. Distribution of average scores between PC1 and PC2 axes of morphological variation between species/subspecies of *Oceanites* genera. Ellipses represent 75% of the variation.

Based on our phylogenetic hypothesis and morphological analyses, and following the general lineage species concept (hereafter GLSC; de Queiroz 1998, 1999, 2007) and the International Code of Zoological Nomenclature (ICZN 1999), we here propose the recognition of the *Oceanites* population of central Chile as a new taxon:

***Description of Oceanites barrosi* sp. nov.**

Andean Storm-Petrel—Golondrina de mar andina (Chilean name)

Holotype

Specimen no. **LACM 25182**, Natural History Museum of Los Angeles County, USA, preserved as a study skin: adult female, collected by Rafael Barros Valenzuela in Río Blanco, Los Andes province, Valparaíso Region, Chile (latitude 32°54'32.06" S, longitude 70°18'15.30 "W, elevation 1,402 m), on 7 April 1924 (Fig. 5). We selected this specimen based on geographic proximity and morphological similarity to the "*barrosi*" specimens sequenced.

FIGURE 5. Type specimen of *O. barrosi*, specimen no. **LACM 25182**, Natural History Museum of Los Angeles County USA, preserved as a study skin: adult female, collected by Rafael Barros Valenzuela in Río Blanco, Los Andes province, Valparaíso Region, Chile (latitude 32°54'32.06"S, longitude 70°18'15.30"W, elevation 1,402 m), on 7 April 1924.

Diagnosis

Typical *Oceanites* structure with (1) small size (Table S3) with short rounded wings, notably short inner wing, and broadly rounded "hand" compared to Hydrobatidae. *Oceanites barrosi* **sp. nov.** wing is, on average, larger than in *O. chilensis* but smaller than in *O. pincoyae*. At the same time, its tail and tarsus measurements are smaller than in *O. chilensis* and larger than in *O. pincoyae* (Table S3). Noticeably smaller than *O. exasperatus* and somewhat smaller than *O. oceanicus* mainly in wing and tail length (Table S3). (2) Restricted white tips on the belly, never as extensive as in *O. galapagoensis*, *O. gracilis*, or *O. pincoyae*, but typically not dark-bellied like *O. chilensis*, *O. oceanites*, and *O. exasperatus*. (3) Bold double pale line on underwing due to pale tipping on underwing coverts.

Underwings are dark in *O. exasperatus* and *O. oceanicus*, and pale tipping not as bold in *O. chilensis*. (4) Square-cut tail with conspicuous white, rectangularly shaped rump patch. (5) In-flight, protruding feet with yellow webs. (6) Well-differentiated genetically. (7) High Andean breeding distribution in central Andes of Chile above treeline. Sexes similar. Supplementary photos in Fig. 6 and Figs S4–S6.

Description of holotype

Color descriptions follow Smithe (1975). Plumage: Upperparts: Entire head, mantle, scapulars, back and upper rump are Blackish-brown (Sepia, Color 119). The longest tertials are narrowly but distinctly edged with white. Upper tail coverts white with white rachis, forming a continuous white, band-shaped rump patch. Some lateral uppertail coverts indistinctly tipped pale brownish. Head similarly Blackish-brown (Sepia, Color 119), showing some pale gray tipping on the forehead, and a whitish-gray loral patch, and narrow so it does not reach the bill. This creates a pale somewhat rectangular area immediately in front of the eye. Underparts: Chin paler and grayer than head. Breast, upper belly, upper flanks, Blackish-brown (Sepia, Color 119). Mid-belly to vent brown with whitish tips, forming a diffuse but noticeable pale belly patch. Crissum from between legs to base of tail entirely Blackish-brown (Sepia, Color 119). Lower flanks and lateral tail coverts white, forming a contiguous white band with the white of the uppertail coverts; this white patch is isolated from the pale lower belly area. Outer tail: Above and below Blackish-brown (Sepia, Color 119), the two outermost feathers, R5 and R6, with white to the bases of inner vanes pointing backward in a triangular shape toward the tail tip.

Upperwing: Lesser coverts, carpal coverts, primary coverts, primaries, and secondaries Blackish-brown (Sepia, Color 119) with narrow pale fringes to the innermost primary coverts and with white fringes to the inner three secondaries. Prominent pale buffy-white wing band on greater secondary coverts extending outward from tertials and inner three secondaries to reach the innermost greater primary coverts. The pale upperwing band is stronger (paler) towards tips of greater secondary coverts.

Underwing: Marginal and lesser underwing coverts, primaries and secondaries Blackish-brown (Sepia, Color 119). Greater and median underwing coverts Blackish-brown (Sepia, Color 119) with whitish tips, forming two parallel pale lines on underwing.

Bare parts: Iris Blackish-brown (from specimen label); bill black; legs and feet black with yellow webs in center bordered with black.

Measurements of holotype

Tarsus 31.7 mm; wing-chord 134 mm; culmen length 11.9 mm; tail 56 mm; mid-toe claw 24.7 mm.

Paratypes

MNHNCL 3500 Male, adult, collected by P. Robinson in Mineral Río Blanco, Aconcagua, Valparaíso Region, Chile (32°54'32"S, longitude 70°18'15"W, elevation 1,400 m), on 15 March 1961. Specimen prepared by P. Robinson. Measurements: tarsus 31.5 mm; wing-chord 134 mm; culmen length 10.8 mm; tail 52 mm; mid-toe claw 24.6 mm.

LACM 25183 Female, adult, collected by Rafael Barros Valenzuela in Río Blanco, Los Andes province, Valparaíso Region, Chile (latitude 32°54'32.06"S, longitude 70°18'15.30"W, elevation 1,402 m), on 8 April 1924. Specimen prepared by Rafael Barros. Measurements: tarsus 32.0 mm; wing-chord 136 mm; culmen length 11.0 mm; tail 56 mm; mid-toe claw 26.6 mm.

MNHNCL 3606 Female, adult, collected by Juan Schlatter on Top of the Cerro Manquehue, Santiago, Región Metropolitana, Chile (latitude 33°21'08''S, longitude 70°34'49''W, elevation 1,630 m), in November 1966. Specimen prepared by Juan Schlatter. Measurements: tarsus 32.5 mm; wing-chord 143 mm; culmen length 10.9 mm; tail 58 mm; mid-toe claw 24.1 mm.

Etymology

The chosen scientific name *barrosi* refers to Rafael Barros Valenzuela (1890–1972) a Chilean ornithologist who first recorded specimens of *Oceanites* around the Andean mountains of Aconcagua, Chile. Rafael Barros was one of the most prolific ornithologists in Chile during the 20th century, and we name this species in recognition of his work. The holotype specimen was collected by him (LACM 25182) on 7 April 1924.

FIGURE 6. Live individual of *Oceanites barrosi* **sp. nov.** captured by Rodrigo Barros in Río Blanco, Los Andes province, Valparaíso Region, Chile (latitude 32°54'S, longitude 70°18'W, elevation 1,400 m), on 9 January 2022.

English name

We propose the name Andean Storm-Petrel due to its unique breeding area. Although a nest has not yet been found, the Andean Storm-Petrel is seen going in and out of high elevation areas during the breeding season, and many recently fledged juveniles have been found in elevations above the city of Santiago (Barros 2017).

Discussion

Phylogenetic analyses

Our analyses resulted in a topology incongruent with plumage-based systematic treatments of *Oceanites* diversity (Fig. 1) and suggested the existence of higher species-level diversity than formally described (Dickinson & Christidis 2015; Howell & Zufelt 2019; Remsen *et al*. 2023). The most obvious rearrangement involves the paraphyletic relationships within *Oceanites oceanicus* and *O. gracilis* complex. The results support the validity of the taxon *O.* (*oceanicus*) *exasperatus*, and its plumage similarity with *O.* (*oceanicus*) *oceanicus* sustains the hypothesis that *exasperatus* is a sibling or cryptic species, contra Howell & Zufelt (2019) who discount the validity of *O.* (*oceanicus*) *exasperatus*. Given our phylogeny and that a sample from North America falls within the *exasperatus* clade, it is likely that only *exasperatus* migrates to the northern hemisphere while all other forms are resident in the southern hemisphere (Fig. 2 and Table 1). The tree topology supports treating *oceanicus*, *chilensis,* and *exasperatus* as separate species. Regardless, genetic divergence within the *Oceanites oceanicus* complex is high (≥3%), exceeding that of many other species-level splits in the family (Nunn & Stanley 1998; Robertson *et al*. 2011; Cibois *et al*. 2015). A similar pattern is observed in *gracilis*, in which its two subspecies do not form a monophyletic group, the taxon *gracilis* being the sister taxon of *pincoyae* and *barrosi* **sp. nov.**, and *galapagoensis* sister species of *oceanicus*. We have only one sample of the taxon *pincoyae*, which was sequenced twice, and we lack full-length sequence data. However, we did PCR-amplify the most informative central region of the Cytb gene, which is essential for correctly placing many taxa in phylogenies (Wiens 2006), and this topology (Fig. 2) also suggests treating *pincoyae* as a separate species with strong genetic divergence (5%). Our phylogeny also confirms the presence of an undescribed taxon in central Chile, which had long been considered part of the subspecies *chilensis* (Harrison *et al*. 2013; Barros 2017). Because *chilensis* represents the most basal taxon of *Oceanites* and does not form a monophyletic group with the populations of central Chile, we therefore described the latter as a new species (see description above).

Morphology and distribution

The morphology-based analysis recognizes size variation between some *Oceanites* species, with *gracilis* and *galapagoensis* the smallest-bodied taxa and *exasperatus* the largest taxon. While *pincoyae* and *chilensis* have differences in size, both present wide overlap with *barrosi* **sp. nov.** Finally, *oceanicus* and *exasperatus* do not show such marked differences. These overlapping levels between species might be explained by similar ecological constraints that do not promote morphological variation (Taylor *et al*. 2019). However, the observed phylogenetic relationships, geographic and genetic distances, and additionally, differences in reproductive phenology by latitude could have promoted allopatric speciation, leading to these cryptic species.

Considering that *Oceanites* are cryptically colored with conservative plumage variation, the best approach to understanding the distribution of each taxon will be the breeding distribution. The new taxon in central Chile appears to breed in a region isolated from *gracilis* to the north and *pincoyae* to the south, all of which are far from the known breeding distribution of *chilensis* (Spear & Ainley 2007; Palma *et al*. 2012a; Howell & Zufelt 2019). The species *Oceanites chilensis* breeds in the Cape Horn region of far southern Chile (Palma *et al*. 2012a), and its dispersion towards the Humboldt current must be reanalyzed with geolocator data as we currently do not know where it spends the non-breeding season (cf. Drucker *et al*. 2020). Most likely, the specimens previously identified as *chilensis* and observed in the Humboldt Current will be found to be the new taxon *barrosi* **sp. nov**. An analysis based on larger samples and genomic analysis may shed light on the speciation process. The at-sea distribution of the taxa *oceanicus* and *exasperatus* is also complex; in our phylogenetic analysis, a specimen from the North Atlantic formed a clade with representatives from Antarctica (see Table 1 of samples and Fig. 2), suggesting that *exasperatus* migrates to the North Atlantic, and that perhaps *oceanicus* is more local. *Oceanites oceanicus* (Kuhl, 1820) does not have a type locality in the original description, although it is based on a life-sized illustration of a bird collected offshore from Buenos Aires, Argentina. Bourne (1964a) suggested that size of the illustration matched that of the Falklands/Malvinas Islands population. Murphy & Beck (1918) designated South Georgia as the type locality. The Falklands/Malvinas and perhaps Isla de Los Estados must also be added to its area of breeding distribution and future analyses should include material from South Georgia. Finally, for *gracilis* and *galapagoensis*, their distribution is more precisely known, with *gracilis* present in the Eastern Pacific in cold waters of the Humboldt Current from Ecuador and central to southern Chile (Spear & Ainley 2007), with breeding in Chungungo Islet, off Chile (29° S) and the Atacama Desert (Barros *et al*. 2020). Because *galapagoensis* is only known from waters around the Galapagos Islands, it presumably breeds in the Galapagos, but nests are not yet known (Medrano *et al*. 2021). It is important to highlight that the clade that includes *gracilis*, *barrosi* **sp. nov.**, and *pincoyae* includes members of populations that are currently classed under the three recognized species in *Oceanites*. This is confusing, considering that in the new arrangement, this clade includes the only continental breeding forms within *Oceanites*, with the caveat that the exact breeding grounds of *barrosi* **sp. nov.** and *pincoyae* are not yet known. However, for *barrosi*, two adult individuals rescued from the lights around Santiago laid eggs before dying (Barros 2017). Also, Murphy (1936) pointed out that many of the specimens captured by Beck in November and December off Valparaíso had greatly enlarged gonads, which suggests that they nest not far from this area. *Oceanites gracilis* breeds largely in the Atacama Desert (Barros *et al.* 2020); while *barrosi* **sp. nov.** clearly breeds in the Andes of central Chile based on multiple lines of evidence; and the breeding area of *pincoyae* is not known but the multiple records on the Argentine side also suggest inland (montane) rather than island breeding sites (Pearman 2000). Present evidence strongly suggests that there are gaps in the breeding distribution between these three taxa: *gracilis* in desert, *barrosi* in alpine habitats in the Andes, and *pincoyae* in isolated taller mountains in northern Patagonia. Similarly, it seems likely that there will be a substantial gap between inland-breeding *pincoyae* and the southern and island-breeding *chilensis*.

Our biogeographic reconstruction suggests a colonization process of the ancestor of *Oceanites* from the Southern Ocean to the Southeast Pacific that generated *O. gracilis*, *O. pincoyae*, and *O. barrosi* **sp. nov.** around 15–18 mya. The colonization of Antarctica occurred around 17 mya and promoted the occurrence of *O. exasperatus* in that continent. Colonization of the Atlantic (*O. oceanicus*) would have occurred from the Southeast Pacific 15 mya ago. However, these patterns should be better understood with a genomic or multilocus approach allowing the divergence time between groups to be evaluated more precisely.

Taxonomy of *Oceanites*

Here we re-evaluate the systematics of *Oceanites* based on a phylogenetic tree with a complete representation of each taxon described for *Oceanites*, six subspecies, and a new population from the central Andes of Chile that we propose as a new taxon. We included specimens sampled close to type localities and a broad representation of biometric data from museums. Our sampling suggests that each formerly described subspecies must be elevated to a species category following the GLSC (de Queiroz 1998, 1999, 2007). Our results show that subspecies within two of the currently recognized *Oceanites* species are polyphyletic. This new phylogenetic hypothesis suggests a new linear sequencing within the genus *Oceanites.* Following the criteria of Remsen *et al.* (2023); this should be as follows:

Oceanites chilensis (Mathews 1934)—Fuegian Storm-Petrel
Oceanites exasperatus (Mathews 1912)—Antarctic Storm-Petrel
Oceanites gracilis (Elliot 1859)—Elliot's Storm-Petrel
Oceanites pincoyae (Harrison *et al.* 2013)—Pincoya Storm-Petrel
Oceanites barrosi **sp. nov.**—Andean Storm-Petrel—Golondrina de mar andina (Chilean name)
Oceanites galapagoensis (Lowe 1921)—White-vented or Lowe's Storm-Petrel
Oceanites oceanicus (Kuhl 1820)—Subantarctic Storm-Petrel

Note that English names used here are those which are officially used now or have been suggested in the recent literature, and these include eponyms. We are using these for convenience of communication and would not oppose the use of other names which may be more informative of the geographic or ecological history of these species.

The species *O. exasperatus* Mathews, 1912 has the type locality of "at sea, off New Zealand" and is described as larger than *oceanicus*. Currently, all Antarctic populations breeding south of the Antarctic Convergence are classified as the larger *exasperatus* (Roberts 1940; Beck & Brown 1972; Pacha *et al.* 2023). However, given the geographical distance, the phylogenetic relationships of other populations of *O. exasperatus* present in Antarctica should be reviewed, particularly in southern Africa and Oceania. Since Wilson's Storm-Petrel is the English name assigned to *O. oceanicus*, we suggest using Antarctic Storm-Petrel for *O. exasperatus*. Murphy & Beck (1918) as well as Bourne (1964b) argued that measurements are variable between southern Atlantic breeding *oceanicus* and *exasperatus*, and they suggested that all populations should be treated as *oceanicus*. Kuhl (1820) named *Procellaria oceanica* from a drawing of a specimen captured near the mouth of the La Plata River during Cook's first expedition (Bourne 1964b), the type locality having subsequently been designated by Murphy & Beck (1918) as South Georgia. The nominate subspecies is, therefore, the breeding form in subantarctic islands including South Georgia, Falkland/Malvinas, and Kerguelen. The name *parvus* (Falla 1937) exists for populations on Kerguelen Island, but apart from a mention in Roberts (1940), this name has not been used subsequently. Given that Wilson's Storm-Petrel is the English name that has been applied to multiple taxa in our current study, and the breeding distribution of *oceanicus* is in subantarctic islands, we consider that the most appropriate name for *O. oceanicus s.s.* is Subantarctic Storm-Petrel.

The Elliot's Storm-Petrel has two allopatric populations, nominate *gracilis* in the Humboldt Current region and the larger and paler form *galapagoensis* of the Galapagos (Lowe 1921). For *O. galapagoensis* we adopt the English name used by Howell & Zufelt (2019) for this population, Lowe's Storm-Petrel. This may require a name change which will require some thought; although Galapagos Storm-Petrel would be obvious, this has been applied in the past to *Hydrobates tethys*. Fuegian breeding populations of *O. chilensis* are smaller than *oceanicus* and named *chilensis* based on a specimen from Wollaston Island, Chile (Mathews 1934). The complex nomenclatural history is noted in Murphy (1936) and Sheard (1943), and clarified in Palma *et al.* (2012a, b).

Until this work, there was no name for central Chilean populations (Mathews 1934; Murphy 1936; Sheard 1943; Spear & Ainley 2007; Palma *et al*. 2012a; Howell & Zufelt 2019). *Oceanites barrosi* **sp. nov.** is similar to *O. pincoyae* and *O. chilensis*. Differences between these species include the extension of white across the belly and underwing coverts. The holotype specimens were previously identified as *O. oceanicus chilensis* but were re-identified as *O. gracilis gracilis* (see Fig. 5) by M. Marin on 4 May 2000 (H.-S. Young, pers. comm.). The extension of white on the belly is a trait that has historically been attributed to *O. gracilis*. Still, newly reviewed material reveals this to be a trait shared to a greater or lesser degree among *gracilis*, *galapagoensis*, *pincoyae*, and *barrosi* **sp. nov.** Our results and new taxonomic arrangement lead to the urgency of discovering the breeding sites of *pincoyae, galapagoensis*, and *barrosi* **sp. nov.** to understand their population sizes and conservation status. It is eye-opening that three of the seven species in *Oceanites* have not yet had their nests described. In all the proposed taxa, the conservation categories should be re-assessed since population sizes and breeding sites are still unknown for several newly recognized species.

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Author contribution HVN, RB, FM, and CEH designed the project and raised funds. HVN CG, KB, and RB were responsible for fieldwork. HVN, TK, and FM conducted the lab analysis. HVN analyzed data and interpreted results. HVN and FM developed the first draft of the manuscript. All authors approved the contents of the manuscript.

Data availability Data are available from the corresponding author on request and will be deposited in Dryad public repository upon acceptance.

Compliance with ethical standards

Ethics statement Field protocols adhered to the local laws of Chile and were approved by the Servicio Agrícola y Ganadero permits N° 9853/2019.

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Supplemental material

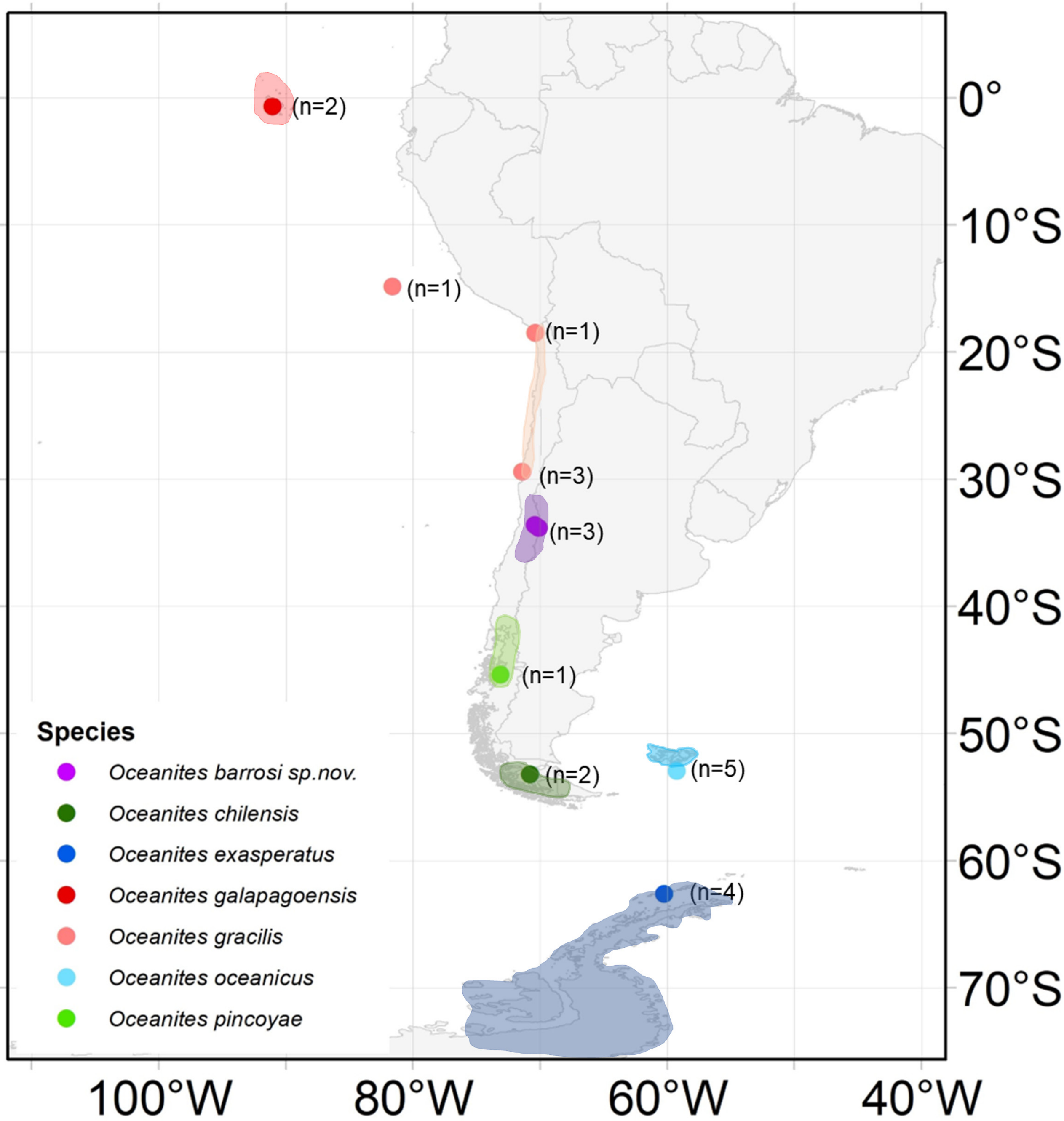

FIGURE S1. Map with the sampling localities (excluding North America) for the genus *Oceanites* included in this study. Colored polygons indicate the approximate breeding areas of each taxon.

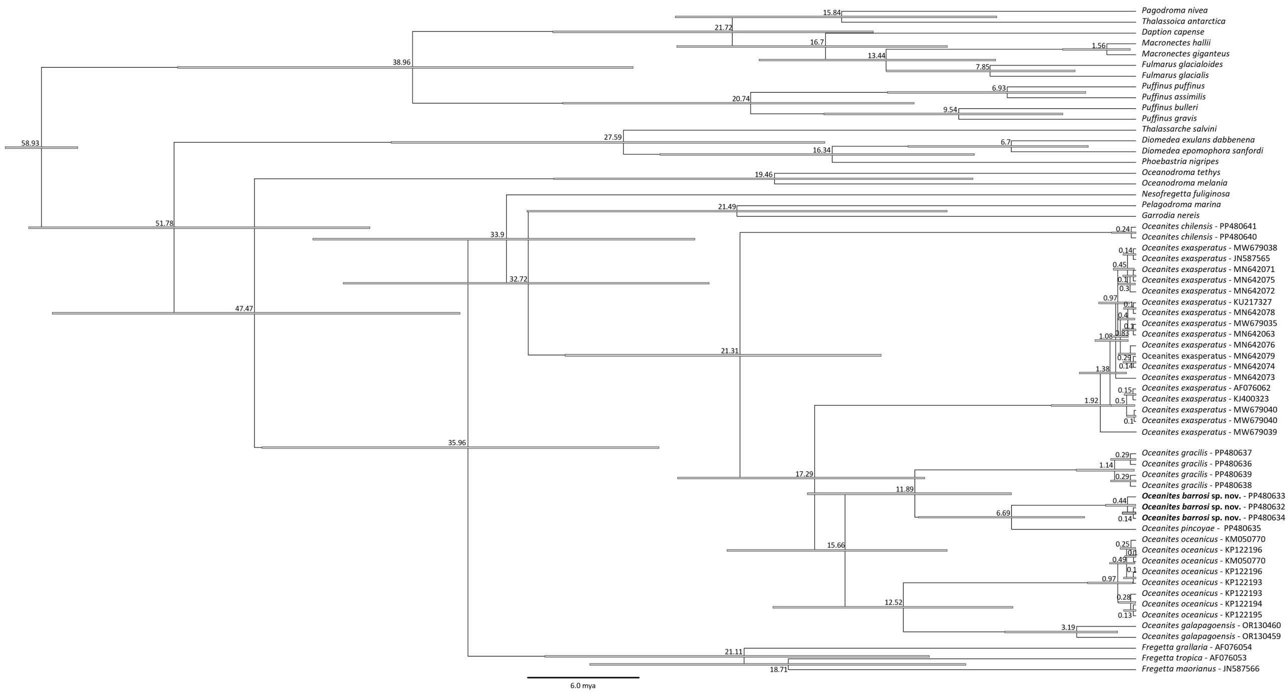

FIGURE S2. Calibrated phylogeny of *Oceanites* and related taxa based on BEAST analysis generated from Cytb sequence. Node numbers are node age in millions of years ago. Dark bars represent 95% highest probability density surrounding divergence times.

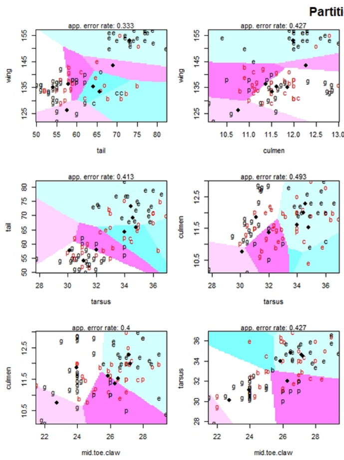

FIGURE S3. Partition plot based on linear discriminant function analysis of morphological data of the genus *Oceanites*.

FIGURE S4. Wing views of live individuals of *Oceanites barrosi* **sp. nov.** captured by Rodrigo Barros in Río Blanco, Los Andes province, Valparaíso Region, Chile (latitude 32°54'S, longitude 70°18'W, elevation 1,400 m), on 9 January 2022. The number in the photo identifies the captured specimen.

FIGURE S5. Ventral view of live individuals of *Oceanites barrosi* **sp. nov.** captured by Rodrigo Barros in Río Blanco, Los Andes province, Valparaíso Region, Chile (latitude 32°54'S, longitude 70°18'W, elevation 1,400 m), on 9 January 2022. The number in the photo identifies the captured specimen.

FIGURE S6. Side view of live individuals of *Oceanites barrosi* **sp. nov.** captured by Rodrigo Barros in Río Blanco, Los Andes province, Valparaíso Region, Chile (latitude 32°54'S, longitude 70°18'W, elevation 1,400 m), on 9 January 2022. The number in the photo identifies the captured specimen.

TABLE S1. Results of principal component analysis of morphological variation between species/subspecies of *Oceanites* genera.

Morphometric variable	PC1	PC2	PC3	PC4	PC5
wing	0.47	-0.07	0.72	-0.17	-0.47
tail	0.49	0.25	0.25	0.25	0.75
culmen	0.30	-0.92	-0.17	-0.04	0.18
tarsus	0.48	0.13	-0.43	0.63	-0.42
mid-toe claw	0.46	0.26	-0.45	-0.72	0.00

TABLE S2. Results of linear discriminant analysis of morphological variation between taxa of *Oceanites*. Accuracy 77.3.

lda class	*barrosi* **sp. nov.**	*chilensis*	*exasperatus*	*galapagoensis*	*gracilis*	*oceanicus*	*pincoyae*
barrosi **sp. nov.**	3	2	1	0	0	2	0
chilensis	2	2	0	0	0	0	0
exasperatus	0	0	21	0	0	2	0
galapagoensis	1	0	0	16	1	0	1
gracilis	0	0	0	1	4	0	0
oceanicus	0	0	0	0	0	1	0
pincoyae	2	1	0	1	0	0	11

TABLE S3. Summary statistics of morphological data of each taxon within *Oceanites*. Data are presented as mean ± standard deviation.

Taxon/ (n° individuals)	Wing	Tail	Culmen	Tarsus	Mid-toe claw
barrosi **sp. nov.** (12)	135.8 ± 4.0	61.3 ± 8.0	11.5 ± 0.5	33.3 ± 1.9	25.6 ± 1.5
chilensis (5)	133.4 ± 4.6	65.7 ± 4.6	11.5 ± 0.4	34.8 ± 1.8	26.5 ± 1.1
exasperatus (22)	152.9 ± 4.7	73.1 ± 4.7	12.0 ± 0.6	34.5 ± 1.4	27.2 ± 1.2
galapagoensis (18)	135.2 ± 3.3	54.1 ± 2.3	11.9 ± 0.7	31.1 ± 0.8	23.9 ± 0.9
gracilis (5)	126.2 ± 2.9	57.6 ± 3.2	10.8 ± 0.7	30.1 ± 1.4	22.7 ± 1.3
oceanicus (5)	143.4 ± 9.2	69.0 ± 4.1	12.3 ± 0.7	34.6 ± 1.1	27.2 ± 1.3
pincoyae (12)	136.3 ± 2.8	57.9 ± 3.0	11.4 ± 0.4	32.0 ± 1.4	26.3 ± 1.1