



Recent diversification in an ancient lineage of Notothenioid fishes (*Bovichtus*: Notothenioidei)

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Abstract

Notothenioids are among the most intensively studied lineages of marine fishes. However, notothenioid research is predominantly focused on the approximately 100 species of Antarctic cryonotothenioids. Far less attention is devoted to the non-Antarctic lineages Bovichtidae, *Pseudaphritis urvillii*, and *Eleginops maclovinus*, all of which originated prior to the diversification of cryonotothenioid species. Here we utilize DNA sequence data from mitochondrial and nuclear genes, as well as meristic trait morphology to investigate the evolutionary history of Bovichtidae. *Bovichtus* is the only polytypic lineage of early diverging non-Antarctic notothenioids providing a unique opportunity to contextualize the diversification dynamics of cryonotothenioids with their non-Antarctic relatives. We find strong evidence that species of *Bovichtus* represent a recent evolutionary radiation with divergence times similar to those estimated among the most closely related species of cryonotothenioids. The divergence in traditional meristic trait morphology among species of *Bovichtus* is consistent with their phylogenetic relationships. The phylogeny of *Bovichtus* implies the wide geographic distribution of species in the clade is likely the result of West Wind drift-driven dispersal. The phylogeny and divergence time estimates results reject a hypothesis that species persistence in *Bovichtus* reflects long periods of evolutionary stasis. Instead, we hypothesize that patterns of extinction and diversification in *Bovichtus* closely mirror those observed in their Antarctic relatives.

Keywords West Wind drift · Historical biogeography · Notothenioidei · Bovichtidae · Adaptive radiation

Introduction

Notothenioids, which dominate the near-shore marine habitats of the Southern Ocean, are one of the most intensively studied lineages of teleost fishes (Cheng and Detrich 2007). This attention is not unwarranted as notothenioids are of critical importance to multi-national fishing interests (Kock 1992; Collins 2010), are a key component of the marine food web dynamics of the Southern Ocean (Eastman 1985a, b;

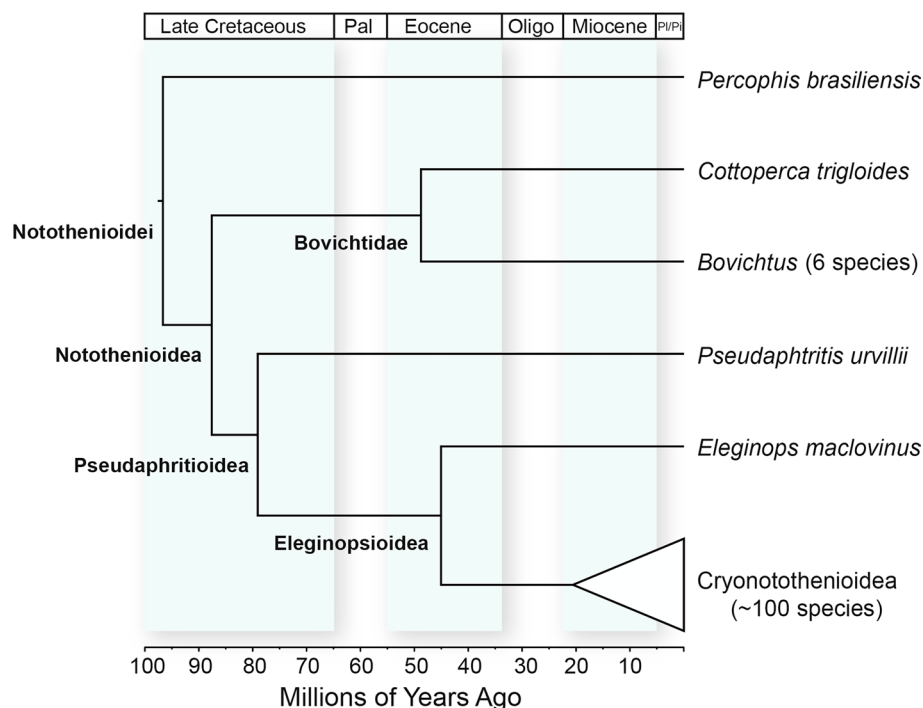
Kock 1985; Barrera-Oro 2002; La Mesa et al. 2004), and are considered a rare example of adaptive radiations among marine fishes (Clarke and Johnston 1996; Near et al. 2012). Although important advances in understanding the evolutionary history and ecology of Antarctic notothenioids have developed over the past 25 years (Eastman 1993; Bargelloni et al. 2000; Near et al. 2012, 2018; Dornburg et al. 2017), far less attention has been devoted toward the development of an evolutionary framework that focuses on the non-Antarctic lineages Bovichtidae, *Pseudaphritis urvillii*, and *Eleginops maclovinus* (Near et al. 2015; Papetti et al. 2016). As result, there is no perspective to compare diversification dynamics of the Antarctic adaptive radiation with other notothenioid lineages.

A notable feature of notothenioid phylogenetic diversity is the presence of non-Antarctic species-depauperate lineages, Bovichtidae (6 species), *Pseudaphritis urvillii*, and *Eleginops maclovinus* that form successive sister lineages of the predominantly Antarctic Cryonotothenioidea (Fig. 1). The divergences times of Bovichtidae and *Pseudaphritis* are consistently placed in the Cretaceous (Near 2004, 2009;

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Fig. 1 Current phylogenetic hypothesis of early diverging notothenioid relationships as discussed in the text. Divergence times reflect those estimated in Near et al. (2015)



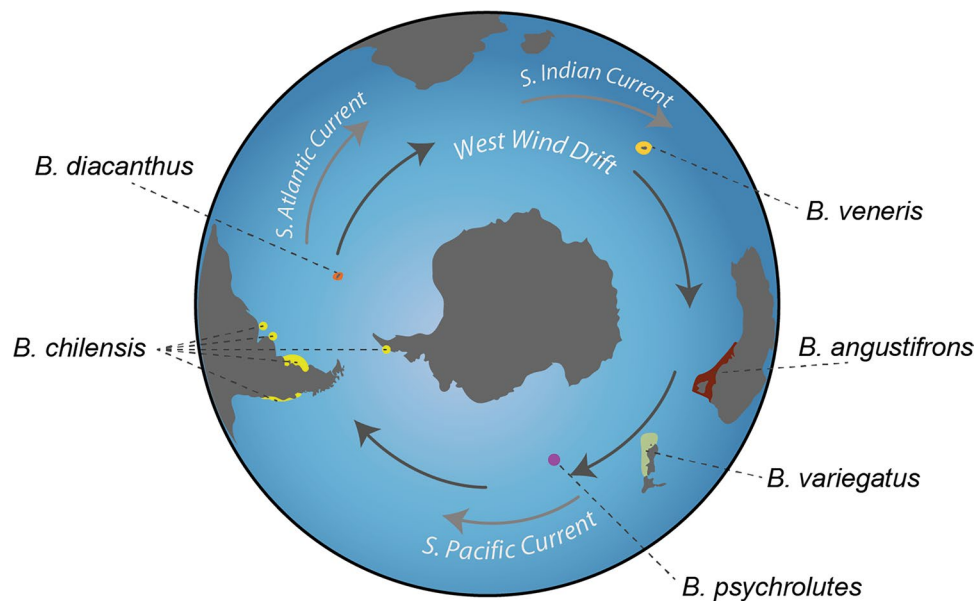
Near et al. 2012, 2015), with their origins hypothesized to have resulted from continental fragmentation in the Southern Hemisphere (DeWitt 1971; Miller 1987; Balushkin 2000; Near et al. 2015). Given that no fossils have been found for these lineages and that both *Cottoperca* and *Pseudaphritis* are monotypic, investigating the evolutionary history of *Bovichtus* represents the only opportunity to explore patterns of speciation in a polytypic ancestrally non-Antarctic notothenioid clade. Inference of a species-level phylogeny for *Bovichtus* has never been attempted (Papetti et al. 2016).

Molecular phylogenetic analyzes that include *Bovichtus* have only included two species, *B. variegatus* and *B. diacanthus*, which resolve as monophyletic with strong node support (Near et al. 2012). All other systematic investigations of *Bovichtus* have used meristic and morphometric traits to assess the distinctiveness of the described species. Regan (1913, pp. 255–257) reviewed eight species of *Bovichtus*, providing descriptions of *B. angustifrons*, *B. chilensis*, and *B. decipiens*. Comparison of meristic data taken from a large number of specimens resulted in *B. argentinus* Mac Donagh and *B. elongatus* Hureau and Tomo being synonymized with *B. chilensis* (Bravo et al. 1999). In a review of the Australasian species of *Bovichtus*, *B. oculus* Hardy was described from a single specimen, *B. decipiens* and *B. roseopictus* Hutton were synonymized with *B. variegatus* Richardson, and *Aurion effulgens* Waite was synonymized with *B. psychrolutes* Gunther (Hardy 1988). A recent study by Balushkin (2016) led to the additional reduction of the number recognized species of *Bovichtus* by synonymizing *B. oculus* with *B. psychrolutes*. While these studies provide an

informed perspective on species diversity, the current lack of a phylogenetic hypothesis challenges the development of a more robust understanding of the evolutionary history of *Bovichtus*.

Collectively, the six recognized species of *Bovichtus* are widely distributed (Fig. 2) from the Pacific and Atlantic coasts of southern South American, the Antarctic Peninsula, Tristan da Cunha, St. Paul Island in the southern Indian Ocean, southern Australia and Tasmania, New Zealand, the Campbell Plateau, and seamounts east of New Zealand in the southern Pacific (Sauvage 1879; Hureau and Tomo 1977; Hardy 1988; Kingsford et al. 1989; Andrew et al. 1995; Bravo et al. 1999; Balushkin 2016). Relaxed molecular clock analyzes have consistently estimated an age for most recent common ancestor (MRCA) of Bovichtidae (*Cottoperca trigloides* and *Bovichtus*) at ~40 Myr. This is nearly twice the age (~23 myr) estimated for the MRCA of the species-rich Cryonotothenioidea (Near et al. 2012, 2015; Dornburg et al. 2017). Given this ancient divergence time between *Cottoperca trigloides* and *Bovichtus* (Fig. 1), it is not clear if the wide geographic distribution of *Bovichtus* is the result of speciation events that occurred in the Paleogene and the living diversity of *Bovichtus* is the result of a gradual accumulation of lineages through time. Alternatively, if the timing of diversification in *Bovichtus* is more recent, it suggests similar patterns of lineage diversification that are observed among species of Antarctic distributed Cryonotothenioidea (Stankovic et al. 2002; Near et al. 2012; Hüne et al. 2015; Dornburg et al. 2017). The absence of a molecular time tree has precluded investigating the evolutionary

Fig. 2 Map showing the geographic distribution of the six recognized species of *Bovichtus*



history and timing of diversification in *Bovichtus*. Over the past 20 years, we have been able to gather specimens from four of the six recognized species of *Bovichtus* for molecular phylogenetic analysis. In this study, we investigate the phylogenetic relationships within *Bovichtus* and timing of diversification in the lineage using a dataset of DNA sequences from mitochondrial and nuclear genes.

Materials and methods

Tissue samples were obtained from specimens collected during several expeditions, and most of these specimens are maintained in museum research collections (Table 1). Qiagen DNeasy Blood and Tissue kits were used to isolate DNA from frozen or ethanol preserved muscle tissues. Four nuclear genes (*enc1*, *Glyt*, *myh6*, and *rag1*) and a single mitochondrial gene (*ND2*) were amplified using PCR and Sanger sequenced using primers published in various studies (Kocher et al. 1995; Lopez et al. 2004; Li et al. 2007). Each of the genes included in this analysis is protein coding, and they were aligned by eye to the dataset used in Near et al. (2012). The alignments were confirmed by examination of the inferred amino acid sequences. No frame shift mutations or DNA substitutions that resulted in stop codons were observed in the aligned sequences. All new sequences were deposited to Genbank MK500763-MK500829. The sampled specimens of *Pseudaphritis urvillii*, *Eleginops maclovinus*, *Dolloidraco longedorsalis*, and *Dissostichus mawsoni* were included in the phylogenetic analyzes, as these taxa represent deep divergences in notothenioid phylogeny and allowed divergence time estimation.

Phylogenies were inferred from each of the five sampled genes using MrBayes v. 3.2 (Ronquist et al. 2012). For each nuclear gene, an HKY substitution model was applied and a GTR+ Γ_4 model was used for the mitochondrial *ND2* gene based on Akaike information criterion-based model selection in ModelTest (Posada and Crandall 1998). The MrBayes v. 3.2 analysis was run for 10^7 generations with two simultaneous runs each with four chains. Convergence and stationarity of the chains were assessed through visual inspection of the chain likelihoods and by monitoring the average standard deviation of the split frequencies between the two runs, which was less than 0.005 after 2×10^6 generations. The first 50% of the sampled generations were discarded as burn-in, and the posterior phylogeny was summarized as a 50% majority-rule consensus tree.

We jointly estimated divergence times and the tree topology for early diverging notothenioids using a multispecies coalescent model with a Yule branching model in the *BEAST2 module in the BEAST v. 2.4 software package (Bouckaert et al. 2014). The uncorrelated lognormal clock model was applied to a partition containing the four nuclear genes and a separate partition containing the *ND2* mitochondrial gene. A “constant populations” was used for the population model, and the population sizes were estimated. An uninformative prior ($1/X$) was used for the strict clock model rate. BEAST v. 2.4 was run four times for 10^8 generations in each run. Based on Akaike information criterion-based model selection, an HKY model was applied to each of the nuclear genes, estimating transition/transversion ratio (κ) and using the empirical nucleotide frequencies. In the GTR+ Γ_4 model applied to the *ND2* partition, the number of gamma categories was 4, using empirical nucleotide frequencies, and estimating the gamma shape parameter.

Table 1 Specimens sampled, location of voucher specimens, and collection locality

Species	Tissue catalog	Specimen voucher	Sampling locality
<i>Bovichtus variegatus</i>	YFTC 1721	None	Otaga Harbour, New Zealand
<i>Bovichtus angustifrons</i>	CSIRO GT 4881	CSIRO H 6958-02	Rockwall at Kingston Beach, Tasmania
<i>Bovichtus angustifrons</i>	CSIRO GT 5613	CSIRO H 7104-08	Rockpool at north end of Pirates Bay (Eaglehawk Neck), Tasmania
<i>Bovichtus angustifrons</i>	CSIRO GT 7322	CSIRO H 7540-02	Shelly Point (Orford), Tasmania
<i>Bovichtus angustifrons</i>	CSIRO GT 4879	CSIRO H 6958-01	Rockwall at Kingston Beach, Tasmania
<i>Bovichtus diacanthus</i>	YFTC 3477	YPM ICH 021534	Atlantic Ocean, Tristan da Cunha
<i>Bovichtus diacanthus</i>	YFTC 3478	YPM ICH 021534	Atlantic Ocean, Tristan da Cunha
<i>Bovichtus chilensis</i>	YFTC 16715	YPM ICH 027476	Pacific Ocean, ~ 25 km north of Fray Jorge National Park, Chile
<i>Bovichtus chilensis</i>	YFTC 16716	YPM ICH 027476	Pacific Ocean, ~ 25 km north of Fray Jorge National Park, Chile
<i>Bovichtus chilensis</i>	YFTC 16717	YPM ICH 027476	Pacific Ocean, ~ 25 km north of Fray Jorge National Park, Chile
<i>Cottoperca trigloides</i>	YFTC 2301	None	Burdwood Banks, Atlantic Ocean
<i>Cottoperca trigloides</i>	YFTC 3925	None	Burdwood Banks, Atlantic Ocean
<i>Cottoperca trigloides</i>	YFTC 3926	None	Burdwood Banks, Atlantic Ocean
<i>Cottoperca trigloides</i>	YFTC 3927	None	Burdwood Banks, Atlantic Ocean
<i>Pseudaphritis urvillii</i>	YFTC 1463	None	Pedler Creek South Australia, Australia
<i>Pseudaphritis urvillii</i>	CSIRO GT 4001	CSIRO 6892-01	Lachlan River, Tasmania
<i>Pseudaphritis urvillii</i>	CSIRO GT 4002	CSIRO 6892-01	Lachlan River, Tasmania
<i>Pseudaphritis urvillii</i>	CSIRO GT 5596	CSIRO 7637-05	Eaglehawk Bay head (Eaglehawk Neck), Tasmania, 0.5 m depth – 43.018713, 147.914897
<i>Eleginops maclovinus</i>	YFTC 3993	YPM ICH 021550	Falkland Islands
<i>Dissostichus mawsoni</i>	YFTC 1226	None	McMurdo Sound, Antarctica
<i>Dolloidraco longedorsalis</i>	YFTC 12894	YPM ICH 020057	Palmer Station, Antarctica

YFTC Yale Peabody Museum Fish Tissue Collection; YPM Yale Peabody Museum, CSIRO Commonwealth Scientific and Industrial Research Organisation

The ages of five nodes were constrained based on previous molecular divergence time estimates for notothenioid fishes (Near et al. 2012, 2015). An exponential distribution with a mean of 1.0 and a minimal age of 23.0 mya was used for the MRCA of Cryonotothenioidea. A normal distributed age prior was used for all other calibrations. The age of the root node (Notothenioidea) was set at 71.4 mya with an average of the distribution set to 0.0 and the standard deviation of 4.0. The most recent common ancestor (MRCA) of *Pseudaphritis urvillii* and Cryonotothenioidea (Pseudaphritioidea) was set to 63.0 mya (mean = 0.0 and standard deviation = 6.5), 42.0 mya for Eleginopsioidea (mean = 0.0 and standard deviation = 5.5), and 39.5 mya for Bovichtidae (mean = 0.0 and standard deviation = 9.0). For each model parameter, plots of the marginal posterior probabilities versus the generation state (generated by the computer program Tracer v. 1.76) were used to assess convergence of parameter estimates and effective sampling of the parameter state space. These plots were also used to assess estimated node heights to their optimal posterior distributions. The resulting tree and log files were combined using the computer program LogCombiner v. 2.4.8. The posterior probability density of the tree files was summarized as a maximum clade credibility tree using TreeAnnotator v. 2.4.8.

Meristic trait data were collected from 17 specimens of *B. diacanthus* collected from Tristan da Cunha (YPM ICH 031,765). Counts of the number of pores in the lateral line, the number of second dorsal fin rays, and the number of anal fin rays were collected following Pequeño and Inzunza (1987). Data for two additional specimens of *B. diacanthus* were taken from Bravo et al. (1999). Meristic data for *B. angustifrons*, *B. chilensis*, *B. psychrolutes*, and *B. variegatus* were taken from Balushkin (2016) and Hardy (1988).

Results

The phylogenies inferred from each of the five sampled genes are entirely consistent with previous molecular analyses of notothenioid relationships (e.g., Near et al. 2012). *Eleginops maclovinus* is resolved as the sister lineage of monophyletic Cryonotothenioidea and Bovichtidae is resolved as monophyletic in each of the five gene trees with strong node support (Figs. 3, 4). However, there is incongruence among the phylogenies concerning the relationship of the species of *Bovichtus* (Figs. 3, 4). With moderate Bayesian node support, *B. angustifrons* and *B. variegatus* are sister species in the *enc1* gene tree (Fig. 3) and in the *ND2*

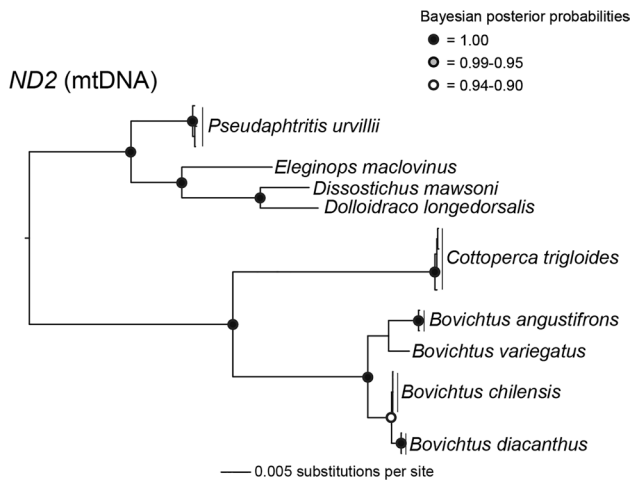


Fig. 3 Bayesian-estimated gene tree topologies for the mitochondrial ND2 gene used in this study. Gray-scale circles indicate Bayesian posterior probabilities

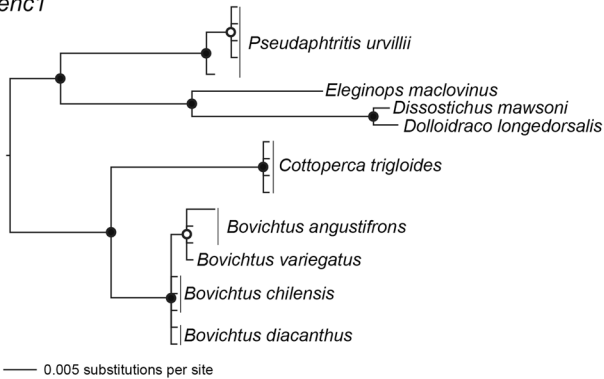
gene tree with Bayesian posterior node support less than 0.90 (Fig. 4). *Bovichtus angustifrons* and *B. chilensis* are strongly supported as sister species in the *myh6* gene tree, and *B. chilensis* and *B. diacanthus* are sister species with moderate node support in the ND2 mitochondrial gene tree, but this clade is strongly supported in the *Glyt* phylogeny (Figs. 3, 4).

The *BEAST2 multispecies coalescent analyzes in BEAST2 scored high ESS values (> 200) for all parameters. The inferred species tree resolves *Bovichtus* as monophyletic and *B. angustifrons* as the sister lineage of all other species of *Bovichtus*. The placement of *B. variegatus* has weak node support, but *B. chilensis* and *B. diacanthus* are strongly supported as sister species (Fig. 5a). The uncertainty in the phylogenetic resolution of *B. angustifrons* and *B. variegatus* is illustrated in the DensiTree plot of the *BEAST2 species tree topologies, which shows a web of relationships among these taxa and the clade containing *B. diacanthus* and *B. chilensis* (Fig. 5b). The posterior age estimate for the MRCA of *Bovichtus* is 4.3 mya [95% highest posterior density (HPD): 1.6–7.9 mya], and

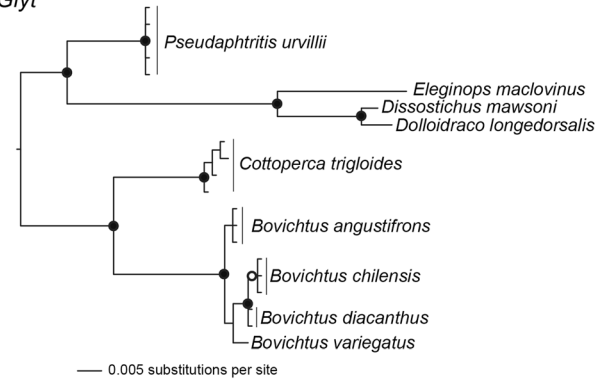
Bayesian posterior probabilities

- = 1.00
- ◐ = 0.99-0.95
- = 0.94-0.90

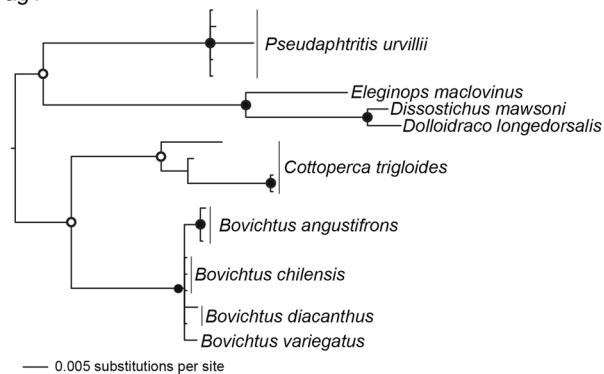
enc1



Glyt



rag1



myh6

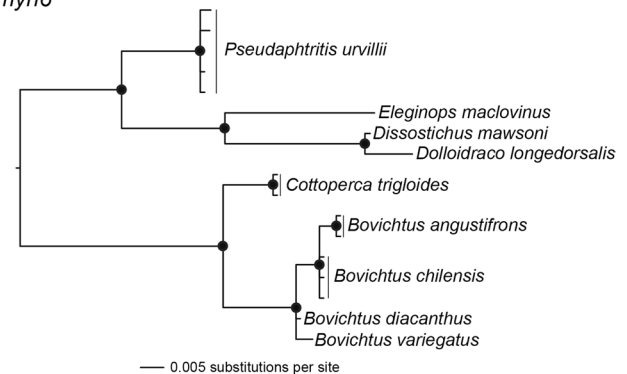
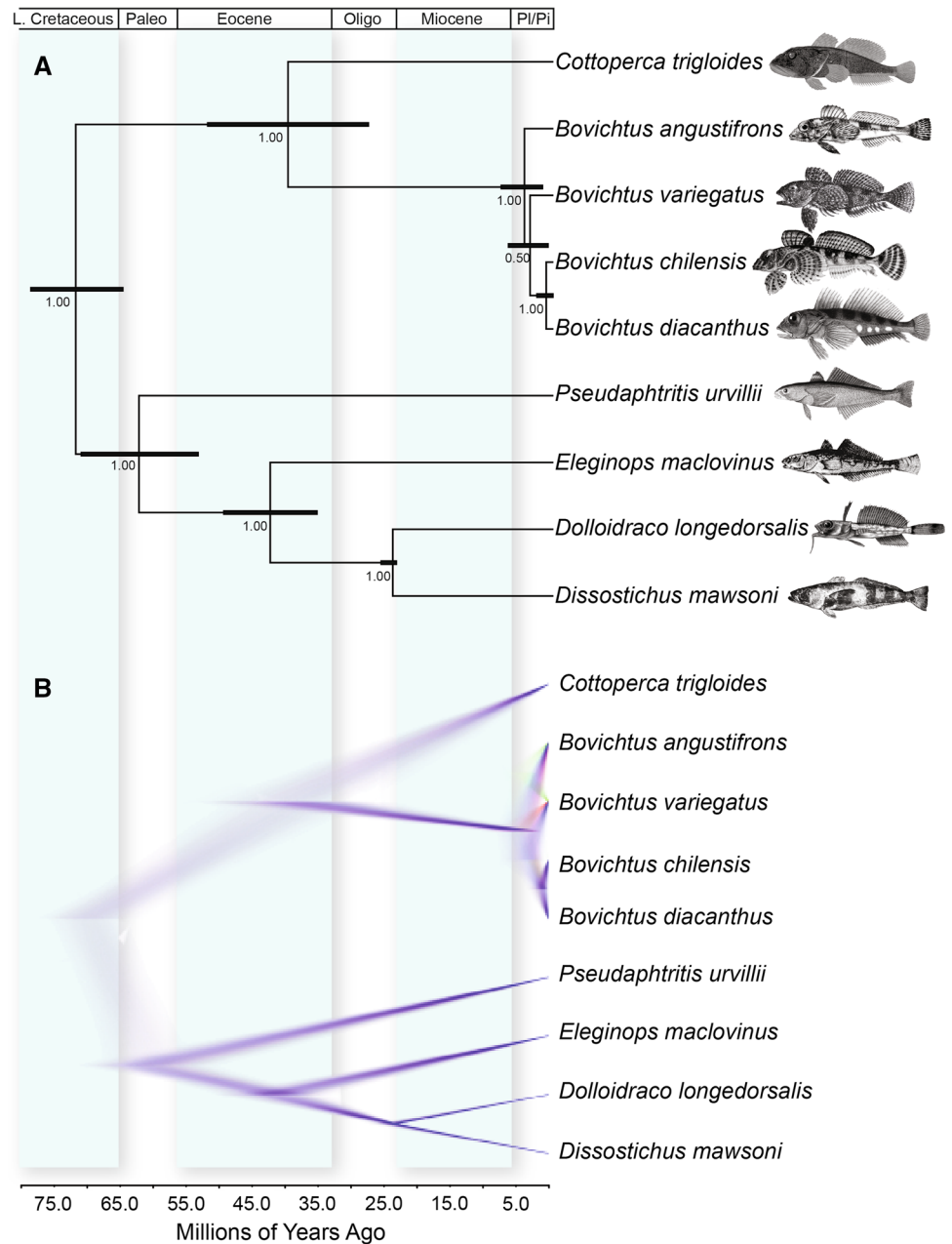


Fig. 4 Bayesian-estimated gene tree topologies for nuclear genes used in this study. Gray-scale circles indicate Bayesian posterior probabilities

Fig. 5 Time calibrated species-tree of *Bovichtus* and other early diverging notothenioid lineages. **a** Species tree of early diverging notothenioids. Bars on nodes indicate 95% highest posterior density intervals of age estimates. Numbers at nodes are Bayesian posterior probabilities. **b** Time calibrated DensiTree plot of species tree topologies depicting gene histories



the age estimate for the clade containing *B. chilensis* and *B. diacanthus* is 1.1 mya (HPD: 0.1–2.5 mya).

The counts of the number of lateral line pores, anal fin rays, and second dorsal fin rays are presented in Tables 2, 3 and 4. The meristic patterns are comparable across the three traits that individual species of *Bovichtus* cluster in one of two groups that are distinguished by relatively low and high counts. *Bovichtus angustifrons* and *B. variegatus* exhibit a similar mean number of lateral line pores and anal fin rays (Tables 2, 3), and the lowest modal counts for second dorsal fin rays (Table 4). The counts for all three traits are very similar in *B. psychrolutes*, *B. chilensis*, and

B. diacanthus, and the trait counts are higher than those in *B. angustifrons* and *B. variegatus* (Tables 2, 3, 4).

Discussion

The inferred phylogeny matches expectations based on comparisons of morphological meristic traits among species of *Bovichtus*. The earliest divergences in *Bovichtus* involve two species with low meristic trait values, *B. angustifrons* and *B. variegatus* (Fig. 5a; Tables 2, 3, 4). The resolution of a clade containing *B. chilensis* and *B. diacanthus* with strong node

Table 2 Counts of lateral line pores in species of *Bovichtus*

Species	Number of lateral line pores																			N	Mean	SD
	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89			
<i>Bovichtus angustifrons</i>	1	4	1	1		5	14	15	18	11	6	4	3							83	78.30	2.51
<i>Bovichtus variegatus</i>		2	3	4	15	19	28	28	31	10	1									141	77.70	1.81
<i>Bovichtus psychrolutes</i>									2	5	25	25	19	20	6	2	3			107	82.55	1.65
<i>Bovichtus chilensis</i>								1		7	11	14	12	10	5	4	2	1		67	82.74	2.00
<i>Bovichtus diacanthus</i>										4	3	5	3	1		3				19	82.32	2.00

N number of specimens, SD standard deviation

Table 3 Counts of anal fin rays in species of *Bovichtus*

Species	Number of anal fin rays							N	Mean	SD
	13	14	15	16	17	18				
<i>Bovichtus angustifrons</i>	5	30	8					43	14.07	0.55
<i>Bovichtus variegatus</i>	12	110	4					126	13.94	0.35
<i>Bovichtus psychrolutes</i>		1	35	18	1	1		56	15.39	0.65
<i>Bovichtus chilensis</i>			17	26	21	7		71	15.25	0.94
<i>Bovichtus diacanthus</i>				11	8			19	15.42	0.51

N number of specimens, SD standard deviation

Table 4 Counts of dorsal fin rays in species of *Bovichtus*

Species	Number of dorsal fin rays					N	Mean	SD
	18	19	20	21	22			
<i>Bovichtus angustifrons</i>		1	7			8	19.88	0.35
<i>Bovichtus variegatus</i>	9	104	13			126	19.03	0.42
<i>Bovichtus psychrolutes</i>			19	41	3	63	20.75	0.54
<i>Bovichtus chilensis</i>		1	19	45	8	73	20.74	0.54
<i>Bovichtus diacanthus</i>		1	6	12		19	20.58	0.61

N number of specimens, SD standard deviation

support is consistent with their similarity in meristic traits that are often used to discover and delimit closely related species of teleosts (Berendzen et al. 2009; Kozal et al. 2017; Near et al. 2017). Although there is no morphological or genetic data available for *B. veneris* Sauvage and there is no genetic data available for *B. psychrolutes*, the high meristics exhibited in the latter provide a viable hypothesis that the species is more closely related to *B. chilensis* and *B. diacanthus*. A comprehensive dataset of morphological and genetic data for all of the recognized species of *Bovichtus* will provide the basis for investigation of phylogenetic relationships and species delimitation.

In addition to needing additional specimens and data to more thoroughly investigate the phylogenetics of *Bovichtus*, the phylogenetic affinity of the bovichtid *Halaphritis platycephala* Last, Balushkin, and Hutchins remains enigmatic. In the description of *H. platycephala*, the species was tentatively classified in Bovichtidae, but it was highlighted that morphological features, such as the narrow spacing of

pelvic fin insertions were shared with Pseudaphritioidea, which is the lineage that contains *Pseudaphritis urvillii*, *Eleginops maclovinus*, and Cryonotothenioidea (Last et al. 2002). There is no available material for molecular analysis, and it remains unclear whether the Australian endemic *H. platycephala* represents an early divergent notothenioid or the sister lineage to Bovichtidae (Fig. 1).

Despite the uncertainty regarding the phylogenetic affinities of bovichtid species not sampled in our analyzes, the divergence time estimates strongly reject the hypothesis that species of *Bovichtus* arose prior to the diversification of cryonotothenioids. Instead, our results demonstrate that the origin of these lineages is temporally coincident with the rise of many of the Antarctic notothenioid species (Near et al. 2012; Dornburg et al. 2017). Similar to cryonotothenioids, there is a long (> 35 Myr) waiting time after the initial divergence of *Cottoperca trigloides* and *Bovichtus*. Most notably, the divergence between *B. diacanthus* and *B. chilensis* occurred within the last 0.5 to 2 million years, suggesting that the

disjunct geographic distribution between these two species reflects recent dispersal between South America and Tristan da Cunha (Figs. 2, 5a).

Species of *Bovichtus* are widely distributed from the Pacific and Atlantic coasts of southern South America, the Antarctic Peninsula, Tristan da Cunha, St. Paul Island in the southern Indian Ocean, southern Australia and Tasmania, New Zealand, the Campbell Plateau, and seamounts east of New Zealand in the southern Pacific (Fig. 2; Sauvage 1879; Hureau and Tomo 1977; Hardy 1988; Kingsford et al. 1989; Andrew et al. 1995; Bravo et al. 1999; Balushkin 2016), raising the question of what biogeographic pathways led to this cosmopolitan distribution. Near et al. (2015) estimated either a South American, or South American + Australian origin for *Bovichtus* based on the distribution of other non-Antarctic notothenioids. However, given the long fuse leading to crown lineage *Bovichtus* estimated in the relaxed molecular clock analyzes and the lack of species diversity in other lineages of non-Antarctic notothenioids (Fig. 5), it is likely that much of the signature of ancient biogeography has been eroded by extinction events. The phylogeny shows that the Australian *B. angustifrons* and the New Zealand endemic *B. variegatus* diverged prior to *B. chilensis* (southern South America) and *B. diacanthus* (Tristan da Cunha). The geography of speciation in *Bovichtus* inferred from our phylogenetic results is consistent with the expectations of West Wind Drift-driven dispersal (Fell 1962; McDowall 1978; Waters 2008). More broadly the evolutionary history of *Bovichtus* aligns with the growing recognition that long-distance dispersal is an important component in explaining the geographic distribution of both terrestrial (Gillespie et al. 2012; Reynolds et al. 2013; Federman et al. 2015; Bauret et al. 2017) and marine (Fraser et al. 2011; Dornburg et al. 2015; Luiz et al. 2015; Carlton et al. 2017; Hou and Li 2018) organisms.

Long-distance dispersal may be particularly important for notothenioids. Several population genetic studies of notothenioid species demonstrate connectivity over hundreds, if not thousands of miles (Matschiner et al. 2009; Damerou et al. 2012; Dornburg et al. 2016a, b), and recent biogeographic analyzes have demonstrated that dispersal from lower latitude peripheral areas into high latitude shelf areas of the Antarctic continent is an important feature of notothenioid evolutionary history (Dornburg et al. 2017). The early life history and behavior of juvenile *Bovichtus* suggest a capacity for long-distance dispersal. The early life stages of *B. diacanthus* and *B. angustifrons* are pelagic silvery-colored fishes that form large schools until they reach a total length of 30 to 60 mm, thereupon the pelagic juveniles move into shallow inshore areas and settle as benthic adults (Sutton and Bruce 1988; Andrew et al. 1995; La Mesa et al. 2010). The connection of early life history to long-distance dispersal is not entirely speculative. A juvenile specimen of *Bovichtus* associating with rafting algae that

was not *B. chilensis* and superficially similar to Australian *B. angustifrons* was discovered off of the coast of South America (Pequeño et al. 2004), providing evidence that *Bovichtus* can use westward flowing currents to cross major ocean basins. As such, long-distance dispersal suggests a mechanism for the widespread geographic distribution and recency of speciation in the evolutionary history of *Bovichtus*.

Our divergence time estimates provide a perspective on the diversification dynamics of early diverging notothenioids. The long phylogenetic branches leading to monotypic lineages such as *Cottoperca trigloides* and *Pseudaphritis urvillii* can be the result of either evolutionary stasis or high levels of background extinction (Stadler 2011), thereby providing little insights into diversification processes (Fig. 1). In contrast, our analyzes of phylogeny and divergence times in *Bovichtus* reveal that species diversity is not the result of early divergences maintained through time, or a gradual accumulation of species over time (Fig. 5a). Instead, species of *Bovichtus* are the result of recent evolutionary diversification. These results are consistent with studies that infer recent speciation in lineages considered to be either ‘living fossils’ or ‘ancient’ relative to their sister lineages (Nagalingum et al. 2011; Near et al. 2014). In the case of *Bovichtus*, the speciation events occur after the middle Miocene climatic optimum, a period of warming that has been implicated in driving extinction within cryonotothenioids (Near et al. 2012). As such, the radiation of *Bovichtus* may well have been driven by ecological opportunities that arose as widespread near-shore communities recovered from climatic perturbation. This hypothesis has also been posited for the diversification of cryonotothenioids (Near et al. 2012; Dornburg et al. 2017), suggesting that diversification among species of *Bovichtus*, and possibly extinction dynamics in other non-cryonotothenioids, may be similar to those of their Antarctic relatives.

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Compliance with ethical standards

Conflicts of interest The authors of this paper have no conflicts of interest.

References

- Andrew TG, Hecht T, Heemstra PC, Lutjeharms JRE (1995) Fishes of the Tristan da Cunha group and Gough Island, South Atlantic Ocean. Ichthyol Bull JLB Smith Inst Ichthol 63:1–43

- Balushkin AV (2000) Morphology, classification, and evolution of notothenioid fishes of the Southern Ocean (Notothenioidei, Perciformes). *J Ichthyol* 40:S74–S109
- Balushkin AV (2016) Systematics of the Antarctic thornfishes of the genus *Bovichtus* (Bovichtidae) of the seamounts of the New Zealand Basin. *J Ichthyol* 56:631–638. <https://doi.org/10.1134/S0032945216050015>
- Bargelloni L, Marcato S, Zane L, Patarnello T (2000) Mitochondrial phylogeny of notothenioids: a molecular approach to Antarctic fish evolution and biogeography. *Syst Biol* 49:114–129
- Barrera-Oro E (2002) The role of fish in the Antarctic marine food web: differences between inshore and offshore waters in the southern Scotia Arc and west Antarctic Peninsula. *Antarctic Sci* 14:293–309
- Bauret L, Gaudeul M, Sundue MA, Parris BS, Ranker TA, Rakotondrainibe F, Hennequin S, Ranaivo J, Selosse MA, Rouhan G (2017) Madagascar sheds new light on the molecular systematics and biogeography of grammitid ferns: New unexpected lineages and numerous long-distance dispersal events. *Mol Phylogenet Evol* 111:1–17
- Berendzen PB, Olson WM, Barron SM (2009) The utility of molecular hypotheses for uncovering morphological diversity in the *Notropis rubellus* species complex (Cypriniformes: Cyprinidae). *Copeia* 2009:661–673
- Bouckaert R, Heled J, Kuhnert D, Vaughan T, Wu CH, Xie D, Suchard MA, Rambaut A, Drummond AJ (2014) BEAST 2: a software platform for Bayesian evolutionary analysis. *PLoS Comput Biol* 10
- Bravo R, Lloris D, Pequeño G, Rucabado J (1999) Revisión de las distintas especies del género *Bovichtus* (Perciformes, Bovichtidae) citadas para el cono sur americano y península Antártica. *Rev Biol Mar Oceanogr* 34:123–137
- Carlton JT, Chapman JW, Geller JB, Miller JA, Carlton DA, McCuller MI, Treneman NC, Steves BP, Ruiz GM (2017) Tsunami-driven rafting: transoceanic species dispersal and implications for marine biogeography. *Science* 357:1402–1405
- Cheng C-HC, Detrich HW (2007) Molecular ecophysiology of Antarctic notothenioid fishes. *Philos Trans R Soc B* 362:2215–2232
- Clarke A, Johnston IA (1996) Evolution and adaptive radiation of Antarctic fishes. *Trends Ecol Evol* 11:212–218
- Collins MA, Brickle P, Brown J, Belchier M (2010) The Patagonian Toothfish: biology, ecology and fishery. *Advances in marine biology*, vol 58, pp 227–300
- Damerou M, Matschiner M, Salzburger W, Hanel R (2012) Comparative population genetics of seven notothenioid fish species reveals high levels of gene flow along ocean currents in the southern Scotia Arc, Antarctica. *Polar Biol* 35:1073–1086
- DeWitt HH (1971) Coastal and deep-water benthic fishes of the Antarctic. In: Bushnell VC (ed) Antarctic map folio series. American Geographical Society, New York, pp 1–10
- Dornburg A, Moore J, Beaulieu JM, Eytan RI, Near TJ (2015) The impact of shifts in marine biodiversity hotspots on patterns of range evolution: evidence from the Holocentridae (squirrelfishes and soldierfishes). *Evolution* 69:146–161
- Dornburg A, Eytan RI, Federman S, Pennington JN, Stewart AL, Jones CD, Near TJ (2016a) Molecular data support the existence of two species of the Antarctic fish genus *Cryodraco* (Channichthyidae). *Polar Biol* 39:1369–1379. <https://doi.org/10.1007/s00300-015-1859-9>
- Dornburg A, Federman S, Eytan RI, Near TJ (2016b) Cryptic species diversity in sub-Antarctic islands: a case study of *Lepidonotothen*. *Mol Phylogenet Evol* 104:32–43. <https://doi.org/10.1016/j.ympev.2016.07.013>
- Dornburg A, Federman S, Lamb AD, Jones CD, Near TJ (2017) Cradles and museums of Antarctic teleost biodiversity. *Nat Ecol Evol* 1:1379–1384. <https://doi.org/10.1038/s41559-017-0239-y>
- Eastman JT (1985a) The evolution of neutrally buoyant notothenioid fishes: their specializations and potential interactions in the Antarctic marine food web. In: Siegfried WR, Condy PR, Laws RM (eds) Antarctic nutrient cycles and food webs. Springer, Berlin, pp 430–436
- Eastman JT (1985b) *Pleuragramma antarcticum* (Pisces, Nototheniidae) as food items for other fishes in McMurdo Sound, Antarctica. *Polar Biol* 4:155–160
- Eastman JT (1993) Antarctic fish biology: evolution in a unique environment. Academic Press, San Diego
- Federman S, Dornburg A, Downie A, Richard AF, Daly DC, Donoghue MJ (2015) The biogeographic origin of a radiation of trees in Madagascar: implications for the assembly of a tropical forest biome. *BMC Evol Biol* 15:216
- Fell HB (1962) West-Wind-drift dispersal of echinoderms in the Southern Hemisphere. *Nature* 193:759. <https://doi.org/10.1038/193759a0>
- Fraser CI, Nikula R, Waters JM (2011) Oceanic rafting by a coastal community. *Proc R Soc B* 278:649–655
- Gillespie RG, Baldwin BG, Waters JM, Fraser CI, Nikula R, Roderick GK (2012) Long-distance dispersal: a framework for hypothesis testing. *Trends Ecol Evol* 27:47–56
- Hardy GS (1988) A revision of *Bovichtus* Cuvier, 1831 (Pisces: Bovichthyidae) from Australasia, with description of a new deepwater species from the New Zealand Subantarctic. *J Nat Hist* 22:1639–1655
- Hou ZG, Li SQ (2018) Tethyan changes shaped aquatic diversification. *Biol Rev* 93:874–896
- Hüne M, González-Wevar C, Poulin E, Mansilla A, Fernández DA, Barrera-Oro E (2015) Low level of genetic divergence between *Harpagifer* fish species (Perciformes: Notothenioidei) suggests a Quaternary colonization of Patagonia from the Antarctic Peninsula. *Polar Biol* 38:607–617. <https://doi.org/10.1007/s00300-014-1623-6>
- Hureau JC, Tomo AP (1977) *Bovichtus elongatus* n.sp., poisson Bovichthyidae, famille nouvelle pour l'Antarctique. *Cybiurn* 3:67–74
- Kingsford MJ, Schiel DR, Battershill CN (1989) Distribution and abundance of fish in a rocky reef environment at the subantarctic Auckland Islands, New Zealand. *Polar Biol* 9:179–186. <https://doi.org/10.1007/BF00297173>
- Kocher TD, Conroy JA, McKaye KR, Stauffer JR, Lockwood SF (1995) Evolution of NADH dehydrogenase subunit 2 in east African cichlid fish. *Mol Phylogenet Evol* 4:420–432
- Kock K-H (1985) Krill consumption by Antarctic notothenioid fishes. In: Siegfried WR, Condy PR, Laws RW (eds) Antarctic nutrient cycles and food webs. Springer, Berlin, pp 437–444
- Kock KH (1992) Antarctic fish and fisheries. Cambridge University Press, Cambridge
- Kozal LC, Simmons JW, Mollish JM, MacGuigan DJ, Benavides E, Keck BP, Near TJ (2017) Phylogenetic and morphological diversity of the *Etheostoma zonistium* species complex with the description of a new species endemic to the Cumberland Plateau of Alabama. *Bull Peabody Mus Nat Hist* 58:263–286. <https://doi.org/10.3374/014.058.0202>
- La Mesa M, Eastman JT, Vacchi M (2004) The role of notothenioid fish in the food web of the Ross Sea shelf waters: a review. *Polar Biol* 27:321–338
- La Mesa M, Caputo V, Eastman JT (2010) Some reproductive traits of the Tristan klipfish, *Bovichtus diacanthus* (Carmichael 1819) (Notothenioidei: Bovichtidae) from Tristan da Cunha (South Atlantic). *Polar Biol* 33:337–346
- Last PR, Balushkin AV, Hutchins JB (2002) *Halaphritis platycephala* (Notothenioidei: Bovichtidae): a new genus and species of temperate icefish from Southeastern Australia. *Copeia* 2002:433–440

- Li CH, Ortí G, Zhang G, Lu GQ (2007) A practical approach to phylogenomics: the phylogeny of ray-finned fish (Actinopterygii) as a case study. *BMC Evol Biol* 7:44
- Lopez JA, Chen WJ, Ortí G (2004) Esociform phylogeny. *Copeia* 2004:449–464
- Luiz OJ, Allen AP, Robertson DR, Floeter SR, Madin JS (2015) Seafarers or castaways: ecological traits associated with rafting dispersal in tropical reef fishes. *J Biogeogr* 42:2323–2333
- Matschiner M, Hanel R, Salzburger W (2009) Gene flow by larval dispersal in the Antarctic notothenioid fish *Gobionotothen gibberifrons*. *Mol Ecol* 18:2574–2587
- McDowall RM (1978) Generalized tracks and dispersal in biogeography. *Syst Zool* 27:88–104
- Miller RG (1987) Origins and pathways possible for the fishes of the Antarctic Ocean. In: Kullander SO, Fernholm B (eds) Proceedings of the Fifth Congress of European Ichthyologists. Swedish National Museum, Stockholm, pp 373–380
- Nagalingum NS, Marshall CR, Quental TB, Rai HS, Little DP, Mathews S (2011) Recent synchronous radiation of a living fossil. *Science* 334:796–799
- Near TJ (2004) Estimating divergence times of notothenioid fishes using a fossil-calibrated molecular clock. *Antarctic Sci* 16:37–44
- Near TJ (2009) Notothenioid fishes (Notothenioidei). In: Hedges SB, Kumar S (eds) The timetree of life. Oxford University Press, New York, pp 339–343
- Near TJ, Dornburg A, Kuhn KL, Eastman JT, Pennington JN, Parnello T, Zane L, Fernandez DA, Jones CD (2012) Ancient climate change, antifreeze, and the evolutionary diversification of Antarctic fishes. *Proc Nat Acad Sci USA* 109:3434–3439. <https://doi.org/10.1073/pnas.1115169109>
- Near TJ, Dornburg A, Tokita M, Suzuki D, Brandley MC, Friedman M (2014) Boom and bust: ancient and recent diversification in bichirs (Polypteridae: Actinopterygii), a relictual lineage of ray-finned fishes. *Evolution* 68:1014–1026. <https://doi.org/10.1111/evo.12323>
- Near TJ, Dornburg A, Harrington RC, Oliveira C, Pietsch TW, Thacker CE, Satoh TP, Katayama E, Wainwright PC, Eastman JT, Beauclieu JM (2015) Identification of the notothenioid sister lineage illuminates the biogeographic history of an Antarctic adaptive radiation. *BMC Evol Biol* 15:109. <https://doi.org/10.1186/s12862-015-0362-9>
- Near TJ, Simmons JW, Mollish J-M, Correa MA, Benavides E, Harrington RC, Keck BP (2017) A new species of logperch endemic to Tennessee (Percidae: Etheostomatinae: *Percina*). *Bull Peabody Mus Nat Hist* 58:287–309. <https://doi.org/10.3374/014.058.0203>
- Near TJ, MacGuigan DJ, Parker E, Struthers CD, Jones CD, Dornburg A (2018) Phylogenetic analysis of Antarctic notothenioids illuminates the utility of RADseq for resolving Cenozoic adaptive radiations. *Mol Phylogenet Evol* 129:268–279. <https://doi.org/10.1016/j.ympev.2018.09.001>
- Papetti C, Windisch HS, La Mesa M, Lucassen M, Marshall C, Lamare MD (2016) Non-Antarctic notothenioids: Past phylogenetic history and contemporary phylogeographic implications in the face of environmental changes. *Mar Genomics* 25:1–9
- Pequeño G, Farías D, Thiel M, Hinojosa I (2004) Peces asociados con la deriva de macroalgas en Aysén, Chile. *Rev Biol Mar Oceanogr* 39:93–99
- Pequeño G, Inzunza AJ (1987) Variabilidad intraespecífica y status sistematico del "torito" *Bovichtys chilensis* Regan 1913 (Osteichthyes, Bovichtthyidae) en Valdivia, Chile. *Bol Soc Biol Concepción* 58:127–139
- Posada D, Crandall KA (1998) Modeltest: testing the model of DNA substitution. *Bioinformatics* 14:817–818
- Regan CT (1913) The Antarctic fishes of the Scottish National Antarctic expedition. *Trans R Soc Edinburgh* 49:229–292
- Reynolds RG, Niemiller ML, Hedges SB, Dornburg A, Puente-Rolon AR, Revell LJ (2013) Molecular phylogeny and historical biogeography of West Indian boid snakes (Chilabothrus). *Mol Phylogenet Evol* 68:461–470
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst Biol* 61:539–542
- Sauvage H-E (1879) Mémoire sur la faune ichthyologique de l'île St Paul. *Arch Zool Exper Gen* 8:1–46
- Stadler T (2011) Inferring speciation and extinction processes from extant species data. *Proc Nat Acad Sci USA* 108:16145–16146
- Stankovic A, Spalik K, Kamler E, Borsuk P, Weglenski P (2002) Recent origin of sub-Antarctic notothenioids. *Polar Biol* 25:203–205
- Sutton CA, Bruce BD (1988) Bovichtidae: thornfishes. In: Neira FJ, Miskiewicz AG, Trnski T (eds) Larvae of temperate Australian fishes Laboratory guide for larval fish identification. University of Western Australia Press, Nedlands, pp 338–343
- Waters JM (2008) Driven by the West Wind Drift? A synthesis of southern temperate marine biogeography, with new directions for dispersalism. *J Biogeogr* 35:417–427

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