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ORIGINAL PAPER

Biogeography of the Antarctic dragonfishes *Acanthodraco dewitti* and *Psilodraco breviceps* with re-description of *Acanthodraco dewitti* larvae (Notothenioidei: Bathydraconidae)

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Abstract

Antarctic dragonfishes (Bathydraconidae) of the suborder Notothenioidei are found only in the Southern Ocean where they diversified in habitats from the surface to the bathypelagic zone thousands of meters deep. Among dragonfishes, the pelagic Gymnodraconinae sister species *Acanthodraco dewitti* and *Psilodraco breviceps* remain poorly known. Although *A. dewitti* is thought to be restricted to Antarctic waters and *P. breviceps* to be endemic to South Georgia Island, several *P. breviceps* specimens have occasionally been reported in coastal Antarctica. Here we investigated the molecular genetic identity of the two species and their geographic distribution. Three mitochondrial genetic markers (*mt-cyb*, *mt-co1*, and *mt-nd2*) identified two dragonfish larvae collected on the West Antarctic Peninsula as *A. dewitti* and showed that all six specimens with available genetic data and reported to be *P. breviceps* collected in Antarctic waters were also *A. dewitti*. These results support the allopatric distribution of the two species, with *P. breviceps* being endemic to South Georgia Island and *A. dewitti* being endemic to Antarctic waters, potentially with a circumpolar distribution. The biogeography of the sister species *A. dewitti* and *P. breviceps* is likely similar to the allopatric distribution of the congeneric sister dragonfish species *Parachaenichthys charcoti* and *P. georgianus.* These considerations suggest that the Antarctic Circumpolar Current may geographically isolate the sub-Antarctic and Antarctic species of both sister species pairs, limiting gene flow and promoting speciation. Furthermore, we provide a detailed description of the *A. dewitti* larvae to supply characteristic morphological features differentiating *A. dewitti* and *P. breviceps* larvae.

Keywords Bathydraconinae · Cygnodraconinae · Andvord bay · Ichthyoplankton

Introduction

The 16 species of Antarctic dragonfishes belong to the suborder Notothenioidei and are found only in the Southern Ocean (Gon and Heemstra 1990; Eastman and Eakin 2000; Duhamel et al. 2014). Dragonfishes are usually slender and small and inhabit a wide variety of habitats, from the ocean surface to the bathypelagic zone thousands of meters deep (Gon and Heemstra 1990; Duhamel et al. 2014; Eastman 2017). Three dragonfish subfamilies (Bathydraconinae, Cygnodraconinae, and Gymnodraconinae) make up the family Bathydraconidae (Duhamel et al. 2014), which molecular genetics recently confirmed to be monophyletic (Near et al. 2018). Dewitt's dragonfish *Acanthodraco dewitti* (Skora 1995), and its sister species *Psilodraco breviceps* (Norman 1938) belong to the subfamily Gymnodraconinae and occupy the pelagic realm, making them rarely observed, poorly known, and therefore possibly mis-identified.

Before the formal description of *A. dewitti* in 1995, some authors suggested that specimens morphologically similar to *P. breviceps* that were collected in Antarctic waters might be a different species than *P. breviceps,* which is thought to be endemic to South Georgia Island (SGI) (e.g., Ekau 1990; Skora and Neyelov 1992; Skora 1995). Upon description of Dewitt's dragonfish based on 12 specimens from South

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Shetland Islands (SSI) on the West Antarctic Peninsula (WAP), Skora ended his description of *A. dewitti* by raising the hypothesis that all reported specimens of *P. breviceps* in Antarctic waters may actually belong to the newly described species *A. dewitti* (Skora 1995). Since then, the separation of both species from each other and their relationships within the Bathydraconidae have become well established morphologically with distinctive opercular spines variations, numbers of lateral lines on the body, and nasal cavity openings in the roof of the mouth (pseudochoanae) which are the most distinctive character of the Gymnodraconinae subfamily (Eastman 1993; Skora 1995; Voskoboinikova and Skora 1996), and molecularly (Derome et al. 2002). Vacchi et al. (2001) described *A. dewitti* from Terra Nova Bay (TNB) and Dettai et al. (2011) from the Dumont d'Urville sea (DDU), supporting Skora's hypothesis on the distribution of Dewitt's dragonfish. In recent years, however, several specimens, identified as *P. breviceps*, were also reported from Antarctic waters (Donnelly and Torres 2008; Smith et al. 2012; Murphy et al. 2017; Piacentino et al. 2018), which contradicts Skora's distribution hypothesis. None of the authors of the latter articles, however, appears to have explored the possibility that their specimens could instead be Dewitt's dragonfish. La Mesa et al. (2000) also described an adult and six *A. dewitti* larvae in the Ross Sea (RS), basing their species identification on Skora's hypothesis of the endemism of *P. breviceps* to South Georgia Island.

In April 2014, we collected two dragonfish larvae in Andvord Bay (AB) on the WAP. Initially we tentatively identified these larvae as *P. breviceps* based on larval fish identification keys by Efremenko (1983) and by Kellermann (1990). The proximity of our samples to the holotype and paratype collection sites for *A. dewitti* (~ 350 km) and the substantial distance of Andvord Bay to South Georgia Island (~ 1.900 km) raised the hypothesis that these larvae might be *A. dewitti* rather than *P. breviceps*. To test this hypothesis and Skora's initial biogeographic hypothesis, we used genetic markers to distinguish the sister species *A. dewitti* and *P. breviceps*. If our larvae were *P. breviceps,* then the species is not endemic to South Georgia Island, inconsistent with Skora's biogeographic hypothesis. If our specimens were *A. dewitti*, however, it is then also possible that other morphologically similar specimens assigned as *P. breviceps* in Antarctic waters might instead be *A. dewitti*, consistent with Skora's biogeographic hypothesis.

Furthermore, the identification of most Antarctic larval fish is based on the comprehensive identification guides by Efremenko (1983) and Kellermann (1990), which were published before the description of *A. dewitti*—the only description of larval *A. dewitti* was performed by La Mesa et al. (2000). To provide additional resources to distinguish *P. breviceps* from *A. dewitti* larvae, we offer here molecular genetic markers to distinguish the two species and a description of our two *A. dewitti* larvae to complement the original larval descriptions available for each species (Efremenko 1983; Kellermann 1990; La Mesa et al. 2000).

Methods

Collection and sampling of larvae

Two *Acanthodraco dewitti* larvae were collected in the night of the 17th to 18th April 2014 in Andvord Bay (AB) (64°46′05" S, 62°44′22" W) on the WAP from the *ARSV Laurence M. Gould.* Both larvae were caught in the same tow using a 500-μm mesh net mounted on a two-by-two meter frame. The net was lowered to approximately 75 m and brought back up for a total fishing time of 29 min and a distance of about 600 m.

Larvae were immediately euthanized in MS-222, fixed in 1% paraformaldehyde (PFA) for 1 h, washed in 100 mM Tris pH 7.5, then progressively dehydrated in increasing ethanol solutions, and stored at room temperature in 80% ethanol until further analysis. All procedures were performed according to protocols approved by the Institutional Animal Care and Use Committees (IACUC) of the University of Oregon (#13-27RRAA).

Genetic analysis

To classify the larvae, DNA was extracted from each specimen using Qiagen DNeasy Blood and tissue Kit (Hilden, Germany). From the most damaged specimen, DNA was extracted from the posterior part of the body, while DNA was extracted from the right eye of the most intact specimen. The two larvae were deposited in the Oregon State University (OSU) Ichthyological Collection (OS 22519; 14.91 mm notochord length (NL) and OS 22520; 16.18 mm NL; damaged) and DNA extracts were deposited in the Ocean Genome Legacy (OGL) collection under the Lot 303 with specimen and extract identification numbers S28602/E30793 and S28603/E30794, respectively (Marine Science Center, Northeastern University, Nahant, MA, USA). Portions of two mitochondrial genetic markers (*mt-co1* (*cytochrome c oxidase 1, mitochondrial*), and *mt-cyb* (alias *cytb*, *cytochrome b, mitochondrial*)), and full mitochondrial genetic marker *mt-nd2* (*NADH dehydrogenase 2, mitochondrial*) were amplified using previously validated primer sets given in Table 1. PCR reactions were performed as previously described (Desvignes et al. 2019a) and amplicons were sequenced in both directions by GENEWIZ (Cambridge, MA, USA). Gene sequences were deposited in NCBI under the accession numbers provided in Table 2. Phylogenetic analyses were performed on Phylogeny.fr web server (Dereeper et al. 2008) by aligning gene sequences

Table 1 Primers used for PCR amplification and Sanger sequencing

Gene Name	Forward primer	Forward primer sequence (5′ to 3′)	Reverse primer	Reverse primer sequence (5′ to 3′)
mt-cyb	L.15053n	CATAAAGAAACCTGAAAYGTGGG	H15915n	AACCTYCGGCCTCCGGTTTACAAGAC
mt-co1	Noto-co1-F1	TCRACYAAYCAYAAAGAYATYGGCAC	Noto-co1-R1	ACTTCWGGGTGRCCRAAGAATCARAA
mt-nd2	ND2-GLN	CTACCTGAAGAGATCAAAAC	ND2-ASN	CGCGTTTAGCTGTTAACTAA

Primer sequences were previously validated in notothenioid species (Kocher 1995; Derome et al. 2002; Dettai et al. 2011; Matschiner et al. 2011; Near et al. 2012; Desvignes et al. 2019b)

Table 2 Overlapping genetic sequences of *Acanthodraco dewitti* and *Psilodraco breviceps*

ID	Capture location	Voucher ID if any	Identification	Genetic identification	*mt-cyb*	*mt-co1*	*mt-nd2*
1	South Georgia Island	N/A	*P. breviceps*	*P. breviceps*	AF490634		
2	Terra Nova Bay	N/A	*A. dewitti*	*A. dewitti*	AF490636		
3	Andvord Bay	OS 22,519	*A. dewitti*	*A. dewitti*	MN160077	MN160073	MN160075
4	Andvord Bay	OS 22,520	*A. dewitti*	*A. dewitti*	MN160078	MN160074	MN160076
5	Marguerite Bay	N/A	*P. breviceps*	*A. dewitti*		KU647487	KR153480
6	McMurdo Sound	N/A	*P. breviceps*	*A. dewitti*		KU647486	KR153372
7	Dumont d'Urville Sea	si155n719	*A. dewitti*	*A. dewitti*		HQ712804	
8	Ross Sea *	P.042658	*P. breviceps*	*A. dewitti*		JN641130	
9	Ross Sea *	P.042669	*P. breviceps*	*A. dewitti*		JN641131	
10	Unknown	YFTC 13,635	*P. breviceps*	*A. dewitti*			HQ170129
11	Unknown	YFTC 11,037	*P. breviceps*	*A. dewitti*			HQ170128

Column 1 refers to the specimen identification in Fig. 2. Column 2 refers to the specimen's capture location and column 3 to the specimen collection voucher designator, if available. Column 4 is the species identification originally made for the specimen upon collection, and column 5 is the genetic identification made in the present study. Columns 6 to 8 contain the accession numbers of the studied sequences

*Exact capture locations are unknown

using MUSCLE, curating the alignment using Gblocks, and constructing a maximum likelihood phylogenetic tree under a GTR + G substitution model implemented in PhyML v3.1. Each phylogenetic analysis was computed using nucleotide sequences generated in this study and a single sequence for each of the other dragonfish species deposited in nucleotide databases. Gene sequences from the Bullhead notothen *Notothenia coriiceps* served as outgroup to anchor the trees. Accession numbers of all sequences used in the phylogenetic analyses are provided in Fig. 1 and in Online Resources 1–3 that contain the curated alignments used for tree reconstructions. To attempt to increase the number of specimens, and potentially generate novel gene sequences for *P. breviceps* or additional specimens of *A. dewitti*, we contacted several collections and colleagues but were unsuccessful in obtaining material suitable for molecular analysis.

Larval description

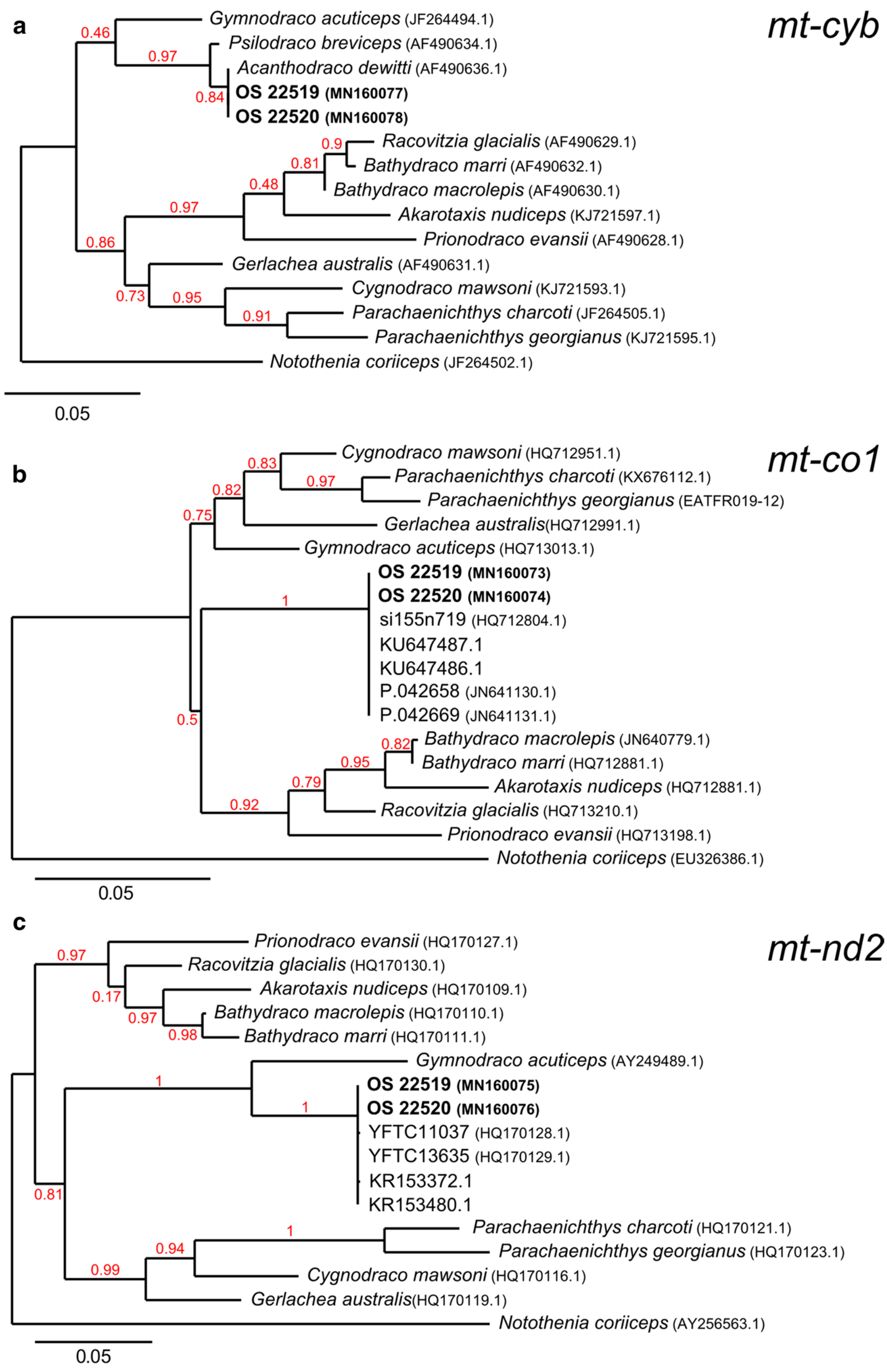
Acanthodraco dewitti larvae were imaged with a Zeiss Discovery V.20 with z-stack ability using the software AxioVision (Zeiss). Image backgrounds were cleaned up using Adobe Photoshop CC 2015. To emphasize larval characters, a schematic drawing of the larvae was created in Adobe Illustrator CC 2019. Because both larvae were in their early flexion stage, we recorded lengths as notochord length (NL), measuring from the tip of the snout to the posterior tip of the notochord. The posterior half of specimen OS 22520 was used for molecular analyses prior to myomere count and therefore was not available for the evaluation of this character.

Results

Acanthodraco dewitti and *Psilodraco breviceps* are molecularly distinct and the larvae collected in Andvord Bay are *Acanthodraco dewitti*

Mining NCBI (National Center for Biotechnology Information, https://www.ncbi.nlm.nih.gov/) and BOLD (Barcode of Life Data, https://www.boldsystems.org/) nucleotide databases for gene sequences attributed to either of the two species retrieved nucleic acid sequences from a total of nine specimens. Eight sequences had been assigned to *A. dewitti* and 34 were labeled as originating from *P. breviceps*

Fig. 1 Maximum likelihood phylogenetic tree reconstructions of our sampled larvae and sequences of other dragonfishes. Gene sequences from the Bullhead notothen *Notothenia coriiceps* served as outgroup to anchor the trees. **a** *mt-cyb* (alias *cytb*), **b** *mt-co1*, and **c** *mt-nd2*. Sequences originating from specimens identified as *A. dewitti* or *P. breviceps* are referred to with the specimen voucher ID and/or with the NCBI accession number of the sequence. Information about all *A. dewitti* and *P. breviceps* specimens and gene sequences included in the study are combined in Table 2. Accession numbers of all the sequences used are given on the figure and the curated alignments used for phylogenetic reconstruction are provided as Online Resources 1–3. Scale bars represent a substitution rate of 0.05 nucleotides per site



(Table 2 for a subset of these sequences). Among these sequences, only two from one specimen could be unambiguously attributed to *A. dewitti* because they originated from a specimen identified by Vacchi et al. in Terra Nova Bay based on a detailed morphological diagnosis (Vacchi et al. 2001; Derome et al. 2002) while other authors did not provide justification for their identification. Only one sequence could be unambiguously attributed to *P. breviceps* because it was the only sequence originating from a specimen actually captured around South Georgia Island (Derome et al. 2002). All other sequences attributed to *P. breviceps* originated from specimens caught in Antarctic waters or from unknown localities and therefore couldn't be considered reliable to test the hypothesis of endemicity of *P. breviceps* to South Georgia

Island. Fortunately, both unambiguously assigned samples for *A. dewitti* and *P. breviceps* had available sequences for the mitochondrial marker *cytochrome b* (*mt-cyb*) (Table 2), making this marker diagnostic for distinguishing the two species.

Phylogenetic tree reconstruction using a single *mt-cyb* sequence from each available dragonfish species (14 out of 16 species) revealed that *P. breviceps* and *A. dewitti* can be molecularly differentiated using the *mt-cyb* genetic marker (Fig. 1a, Online Resource 1). In addition, *mt-cyb* sequences from our larval specimens captured in Andvord Bay along the WAP grouped with the reference sequence for *A. dewitti* (Fig. 1a, Online Resource 1), demonstrating that these larvae were *A. dewitti*.

All Antarctic specimens are *Acanthodraco dewitti*

To further test the hypothesis of the endemicity of *Psilodraco breviceps* to South Georgia Island and of *Acanthodraco dewitti* to Antarctic waters, we questioned whether the other six reports of *P. breviceps* in Antarctic waters for which sequencing data are publicly available may instead be *A. dewitti*. Using two additional mitochondrial genetic markers (i.e., *cytochrome c oxidase 1* (*mt-co1*), and *NADH dehydrogenase 2* (*mt-nd2*)) developed for their low level of intraspecific polymorphism but significant interspecific polymorphism making them classically used for species identification (Kocher 1995; Derome et al. 2002; Dettai et al. 2011; Matschiner et al. 2011; Near et al. 2012; Desvignes et al. 2019b), we were able to test each specimen identified as either *A. dewitti* or *P. breviceps*. For both genes, even without a representative sequence from *P. breviceps*, the absence of divergence in *mt-co1* sequences between our *A. dewitti* larvae and all other specimens (Fig. 1b, Online Resource 2) and the very low level of divergence in *mt-nd2* sequences (Fig. 1c, Online Resource 3) strongly suggest that all these specimens are of the same species as our larvae; therefore we conclude that all six are *A. dewitti* (Fig. 2).

Description of two early life stages of *Acanthodraco dewitti*

Both larvae (OS 22519, 14.91 mm NL, Fig. 3a; and OS 22520, 16.18 mm NL, Fig. 3b) are in an early flexion stage (the posterior end of the notochord has started to bend dorsally) and both specimens have a similar pigmentation pattern. We counted 53 myomeres (m in Fig. 3e) in the smaller specimen (OS 22519). Small teeth are already present in the upper and lower jaws (Fig. 3e). In both specimens, the head lacks spines, which are characteristically numerous in the adults (Skora 1995; Voskoboinikova and Skora 1996; Vacchi et al. 2001). The pelvic, dorsal, and anal fins are not yet developed in both specimens, but a large larval fin fold surrounds the body (Fig. 3e). The caudal fin has started to develop and the haemal arch of preural centrum 1, the parhypural, two hypural plates, and the anlagen of nine caudal fin rays (cfr) are present (but not visible in Fig. 3).

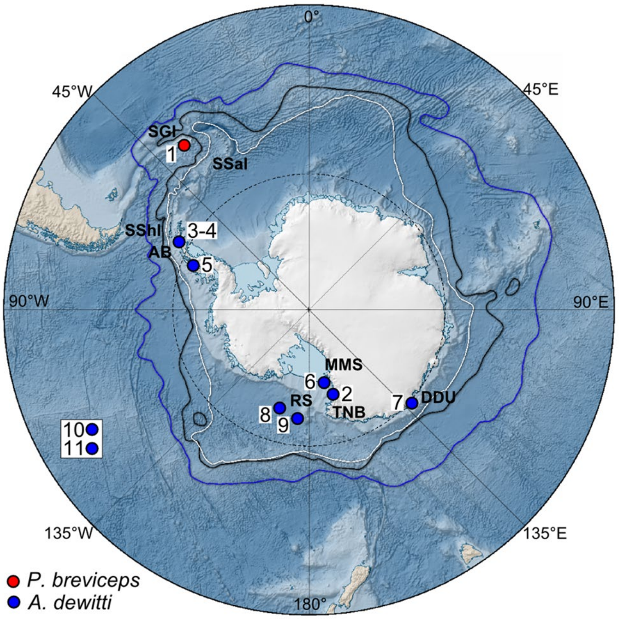


Fig. 2 *Acanthodraco dewitti* and *Psilodraco breviceps* biogeography. Locations of capture of the 11 specimens incorporated in this study. Capture locations are precisely mapped from GPS coordinates, except for specimens 8 to 11, for which imprecise (8, 9) or no collection data (10, 11) are available. Species identification originate from the genetic analysis presented in Fig. 1 and differ from the identification made upon collection of some specimens. Information about all *A. dewitti* and *P. breviceps* specimens included in the study are combined in Table 2. The dashed black line represents the Antarctic Circle, the white line represents the Southern boundary of the Antarctic Circumpolar Current, the black line represents the Southern Antarctic Circumpolar Current Front, and the blue line represents the Polar Front. The map was made using the GIS Quantarctica package (Matsuoka et al. 2018). Localities abbreviations: *AB* Andvord Bay, *DDU* Dumont D'Urville Sea, *MMS* McMurdo Sound, *RS* Ross Sea, *SGI* South Georgia Island; *SSaI* South Sandwich Islands, *SShI* South Shetland Islands, *TNB* Terra Nova Bay

The single nostril (n) is large and occupies laterally the entire space between the anterior ethmoid region (e) and the eye (Fig. 3c). The internal nostrils, or pseudochoanae, a characteristic for the species of the Gymnodraconinae subfamily (Skora 1995), could not be observed. The head is heavily pigmented with large pigment fields in the parietal (p) and frontal (f) regions (Fig. 3c, e). The posterior part of the skull has a field of pigment cells that extends to the epaxial muscle portion of the first six to seven myomeres (Fig. 3c). The distal tip of the ethmoid region and the skin over the premaxilla (pmx) (Fig. 3e) are also pigmented. The pigmentation on the lower jaw is extensive (Fig. 3d). A line of elongated melanophores follows laterally the entire length of the dentary (d) (Fig. 3d, e). The retroarticular (ra) at the posterior end of the lower jaw is characterized by two melanophores (Fig. 3d, e). The skin between the two branches of the dentary is pigmented in its anterior half (Fig. 3d). The pigmentation on the preopercle (pop) and opercle (op) is irregular with some melanophores following a dorsoventral direction. A band of melanophores runs dorsoventrally on the cleithrum (cl) (Fig. 3c). A few large melanophores occupy the base of the small pectoral fin anlagen (Fig. 3d, e). The peritoneal melanophores on the dorsal region of the abdomen (dab) follow the gut and end anterior to the vent where they meet the ventral series of peritoneal abdominal melanophores (vab). The ventral row of large abdominal melanophores starts at the symphysis of the cleithra and forks laterally on the abdomen towards the anus, leaving the ventral midline of the abdomen unpigmented (Fig. 3d). The trunk and the caudal peduncle (cp) are unpigmented (Fig. 3e).

Based on the descriptions of *P. breviceps* by Efremenko (1983) and by Kellerman (1990), the two sister species have slight differences in the pigmentation pattern. Most notably, our *A. dewitti* specimens lack pigmentation at the base of the caudal fin rays. The description of the six larval specimens of *A. dewitti* by La Mesa et al. (2000) is difficult to compare to what we found in our material. Although the schematic drawings provided suggest a similar pigmentation pattern (La Mesa et al. 2000), some details differ and make a thorough comparison challenging, most notably the ventral abdominal pigmentation (see Fig. 3a in La Mesa et al. (2000)) which is absent in our specimens that are also of a smaller size. All bones of the opercular series in adult *A. dewitti* possess spines (Skora 1995; Vacchi et al. 2001) and

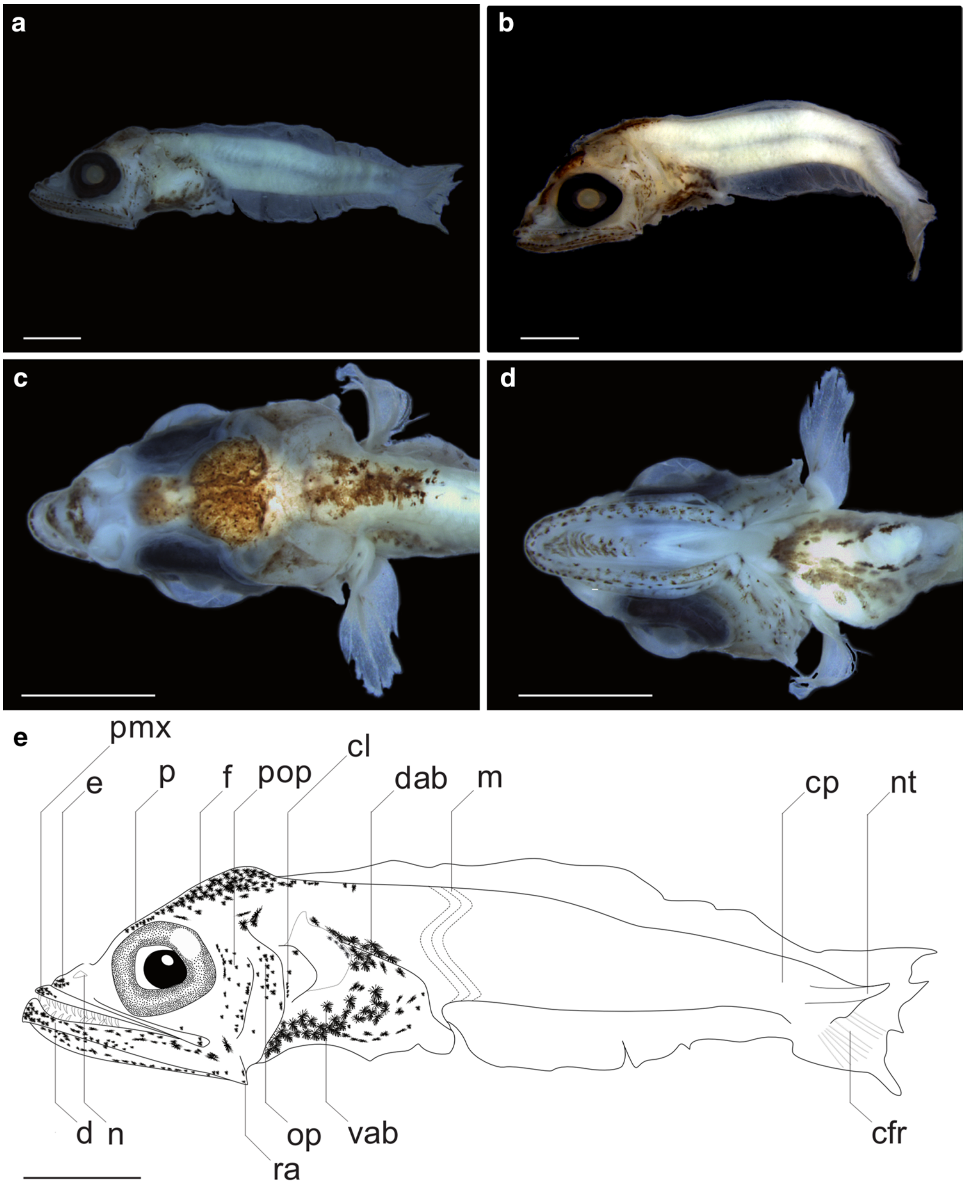


Fig. 3 *Acanthodraco dewitti* larvae OS 22,519 (14.91 mm NL) and OS 22,520 (16.18 mm NL). **a** Left lateral view of OS 22,519. **b** Left lateral view of OS 22,520, before the posterior half was used for DNA extraction. **c** Dorsal view of the head and first few myomeres of OS 22,519. **d** Ventral view of the head and abdomen of OS 22,519. **e** Schematic drawing of the left lateral view of OS 22,519. *cfr* caudal fin rays, *cl* cleithral region of pectoral girdle, *cp* caudal peduncle, *d* dentary, *dab* dorsal abdominal region, *e* ethmoidal region, *f* frontal region, *m* dotted line indicates three representative myosepta of the mid-trunk region, *n* nostril, *nt* notochord, *op* opercular region, *p* parietal region, *pmx* premaxilla, *pop* preopercular region, *ra* retroarticular, *vab* ventral abdominal region. Scale bar corresponds to 2 mm in all panels

larger larval specimens (21.0 mm and 24.6 mm) have an opercular ridge (see Fig. 3b, c in La Mesa et al. (2000)) that could not be observed in our specimens. Our two specimens appear to be at a younger stage than those of La Mesa et al. (2000) and do not show any opercular spines. Kellermann (1990) did not describe spines on any head bones in the larvae of the sister species *P. breviceps* but a strong ridge ending in a flat spine is present in adult specimens (Gon and Heemstra 1990).

It is thus uncertain whether differences between the specimens described by La Mesa et al. (2000) and our two individuals are based on individual or population variations or could be attributed to different preservation methods that can influence pigmentation retention (Schnell et al. 2016).

Discussion

In April 2014, we captured two dragonfish larvae on the West Antarctic Peninsula that were morphologically similar to both of the two sister species *Psilodraco breviceps* and *Acanthodraco dewitti*. Using molecular markers and sequences deposited in nucleotide databases, we showed first, that the two sister species *P. breviceps* and *A. dewitti* can be genetically differentiated. We next demonstrated that the two larvae we collected on the WAP have nucleotide sequences identical to *A. dewitti,* not *P. breviceps*. Third, using the two *A. dewitti* larvae caught on the WAP and additional molecular markers, we demonstrated that all specimens with available genetic data captured in coastal Antarctica and identified as *P. breviceps* had mitochondrial gene sequences identical to those of an unambiguous *A. dewitti* specimen and to our *A. dewitti* larvae. This result supports the hypothesis raised by Skora (1995) that *P. breviceps* is not found in Antarctic waters and that similar specimens found in Antarctica are instead *A. dewitti*. We therefore conclude that *P. breviceps* has never been unambiguously captured in Antarctica and can still be considered endemic to South Georgia Island. While genetic data are lacking, results also revealed that no individuals unambiguously identified as *A. dewitti* have been collected north of the Southern Antarctic Circumpolar Current Front (sACCf). Therefore *A. dewitti* is possibly endemic to Antarctic waters, potentially with a circumpolar distribution.

The possible allopatric distribution of the Gymnodraconinae sister species *A. dewitti* and *P. breviceps* resembles the allopatric distribution of the two Cygnodraconinae sister species *Parachaenichthys charcoti* and *Parachaenichthys georgianus,* which are endemic to the WAP and South Georgia Island, respectively (Gon and Heemstra 1990; Duhamel et al. 2014; La Mesa et al. 2017). In both cases, while all species occur south of the Polar Front (blue line on Fig. 2), within each species pair, sister species are separated by the Southern Antarctic Circumpolar Current Front (sACCf) and the Southern boundary of the Antarctic Circumpolar Current (sbACC) (Black and white lines on Fig. 2, respectively) (Matsuoka et al. 2018). The Antarctic Circumpolar Current flowing between sub-Antarctic islands and Antarctica may represent an oceanic barrier separating *A. dewitti* from its sister species *P. breviceps*, and *P. charcoti* from its sister *P. georgianus*.

In the case of *P. charcoti* and *P. georgianus*, La Mesa et al. (2017) suggested that the short pelagic larval phase of both species and local current restricting their distribution to inshore waters, may have contributed to the speciation of the sister taxa. While the length of the pelagic larval phase in *P. breviceps* and *A. dewitti* is to our knowledge unknown, reported captures of *A. dewitti* larvae and adults were all made inshore (Skora 1995; Frolkina et al. 1998; La Mesa et al. 2000; Vacchi et al. 2001; Murphy et al. 2017; and present study). Therefore, it is possible that the same biotic and abiotic factors isolating the *Parachaenichthys* species pair (i.e., short pelagic larval phase and oceanic currents) could also contribute to the speciation of *A. dewitti* and *P. breviceps* by geographically isolating the sister species and limiting gene flow.

Additional analyses of larval and adult specimens of both species, and from diverse capture locations, are needed to understand with more precision the characteristics that define each species, their development, and the contribution of life history and oceanic currents in the speciation of these elusive sister species.

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Author contributions Study concept and design: TD and PK. Acquisition of data: TD and PK. Analysis and interpretation of data: TD, JHP, PK. Wrote the manuscript: TD and PK. Critical revision of the manuscript: TD, JHP, PK. Obtained funding: TD and JHP. Study supervision: TD.

Data availability All samples and data generated or analyzed during this study are included in this published article (and its Online Resources), deposited in NCBI, at Oregon State University Ichthyological Collection (Corvallis, OR, USA), and at the Ocean Genome Legacy collection (Marine Science Center, Northeastern University, Nahant, MA, USA).

Compliance with ethical standard

Conflict of interest The author(s) declare no competing interests.

References

Dereeper A, Guignon V, Blanc G et al (2008) Phylogeny.fr: robust phylogenetic analysis for the non-specialist. Nucleic Acids Res 36:W465–469. https://doi.org/10.1093/nar/gkn180

Derome N, Chen W-J, Dettaï A et al (2002) Phylogeny of Antarctic dragonfishes (Bathydraconidae, Notothenioidei, Teleostei) and related families based on their anatomy and two mitochondrial genes. Mol Phylogenet Evol 24:139–152. https://doi.org/10.1016/S1055-7903(02)00223-3

Desvignes T, Batzel P, Sydes J et al (2019a) miRNA analysis with Prost! reveals evolutionary conservation of organ-enriched expression and post-transcriptional modifications in three-spined stickleback and zebrafish. Sci Rep 9:3913. https://doi.org/10.1038/s41598-019-40361-8

Desvignes T, François NRL, Goetz LC et al (2019b) Intergeneric hybrids inform reproductive isolating barriers in the Antarctic icefish radiation. Sci Rep 9:5989. https://doi.org/10.1038/s41598-019-42354-z

Dettai A, Lautredou A-C, Bonillo C et al (2011) The actinopterygian diversity of the CEAMARC cruises: Barcoding and molecular taxonomy as a multi-level tool for new findings. Deep Sea Res II 58:250–263. https://doi.org/10.1016/j.dsr2.2010.05.021

Donnelly J, Torres JJ (2008) Pelagic fishes in the Marguerite Bay region of the West Antarctic Peninsula continental shelf. Deep Sea Res II 55:523–539. https://doi.org/10.1016/j.dsr2.2007.11.015

Duhamel G, Hulley P-A, Causse R et al (2014) Biogeographic patterns of fish. In: De Broyer C, Koubbi P, Griffiths H, et al. (eds) Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, pp 328–362

Eastman JT (2017) Bathymetric distributions of notothenioid fishes. Polar Biol 40:2077–2095. https://doi.org/10.1007/s00300-017-2128-x

Eastman JT (1993) Antarctic fish biology—evolution in a unique environment. Academic Press, San Diego

Eastman JT, Eakin RR (2000) An updated species list for notothenioid fish (Perciformes; Notothenioidei), with comments on Antarctic species. Arch Fish Mar Res 48:11–20

Efremenko FN (1983) Illustrated guide to fish larvae of the Southern Ocean. SCAR. SCOR. IABO. ACMRR

Ekau W (1990) Demersal fish fauna of the Weddell Sea, Antarctica. Antarct Sci 2:129–137. https://doi.org/10.1017/S0954102090000165

Frolkina GA, Konstantinova MP, Trunov IA (1998) Composition and characteristics of ichthyofauna in pelagic waters of South Georgia (Subarea 48.3). CCAMLR Sci 5:125–164

Gon O, Heemstra P (eds) (1990) Fishes of the Southern Ocean. J.L.B Smith Institute of Ichthyology, Grahamstown

Kellermann A (1990) Catalogue of larval Antarctic fishes. Ber Polarforsch 67:45–136

Kocher T (1995) Evolution of NADH dehydrogenase subunit 2 in east african cichlid fish. Mol Phylogenet Evol 4:420–432. https://doi.org/10.1006/mpev.1995.1039

La Mesa M, Granata A, Guglielmo L, Vacchi M (2000) First description of larvae of Acanthodraco dewitti in the Ross Sea, Antarctica. J Fish Biol 57:163–166. https://doi.org/10.1111/j.1095-8649.2000.tb02252.x

La Mesa M, Riginella E, Jones CD (2017) Early life history traits and geographical distribution of Parachaenichthys charcoti. Antarct Sci 29:410–416. https://doi.org/10.1017/S0954102017000189

Matschiner M, Hanel R, Salzburger W (2011) On the origin and trigger of the notothenioid adaptive radiation. PLoS ONE 6:e18911. https://doi.org/10.1371/journal.pone.0018911

Matsuoka K, Skoglund A, Roth G (2018) Quantarctica . Norwegian Polar Inst. https://doi.org/10.21334/npolar.2018.8516e961

Murphy KR, Kalmanek EA, Cheng C-HC (2017) Diversity and biogeography of larval and juvenile notothenioid fishes in McMurdo Sound, Antarctica. Polar Biol 40:161–176. https://doi.org/10.1007/s00300-016-1939-5

Near TJ, Dornburg A, Kuhn KL et al (2012) Ancient climate change, antifreeze, and the evolutionary diversification of Antarctic fishes. Proc Natl Acad Sci USA. https://doi.org/10.1073/pnas.1115169109

Near TJ, MacGuigan DJ, Parker E et al (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

Norman JR (1938) Coast fishes. Part III. The Antartic zone. Discov Rep 18:1–105. https://doi.org/10.5962/bhl.part.19412

Piacentino GLM, Moreira E, Barrera-Oro E (2018) Early stages of notothenioid fish from Potter Cove, South Shetland Islands. Polar Biol 41:2607–2613. https://doi.org/10.1007/s00300-018-2366-6

Schnell NK, Konstantinidis P, Johnson GD (2016) High-proof ethanol fixation of larval and juvenile fishes for clearing and double staining. Copeia 104:617–622. https://doi.org/10.1643/CI-15-382

Skora KE (1995) Acanthodraco dewitti gen. et sp. n. (Pisces, Bathydraconidae) from Admiralty Bay (King George Island, South Shetland Islands, Antarctica). Arch Fish Mar Res 42:283–289

Skora KE, Neyelov AV (1992) Fish of Admiralty Bay (King George Island, South Shetland Islands, Antarctica). Polar Biol 12:469–476. https://doi.org/10.1007/BF00243118

Smith PJ, Steinke D, Dettai A et al (2012) DNA barcodes and species identifications in Ross Sea and Southern Ocean fishes. Polar Biol 35:1297–1310. https://doi.org/10.1007/s00300-012-1173-8

Vacchi M, La Mesa M, Ozouf-Costaz C (2001) First occurrence of Acanthodraco dewitti Skora, 1995 (Notothenioidei, Bathydraconidae) in the Ross Sea. Polar Biol 24:471–472. https://doi.org/10.1007/s003000100239

Voskoboinikova OS, Skora KE (1996) Comparative osteology of Acanthodraco dewitti and relationships within the gymnodraconins (Pisces: Bathydraconidae). Zoosystematica Ross 5:203–208