Polar Biol (2002) 25: 384–390
DOI 10.1007/s00300-002-0358-y

ORIGINAL PAPER

M. La Mesa · M. Vacchi · T. Iwami · J.T. Eastman

Taxonomic studies of the Antarctic icefish genus *Cryodraco* Dollo, 1900 (Notothenioidei: Channichthyidae)

Accepted: 7 January 2002 / Published online: 7 March 2002
© Springer-Verlag 2002

Abstract Based on a meristic and morphometric study of 101 specimens, we recognise 2 valid species in the Antarctic channichthyid genus *Cryodraco*: *Cryodraco antarcticus* Dollo, 1900 and *C. atkinsoni* Regan, 1914. Although the species overlap in most meristic and morphometric characters, we have distinguished several reliable characters for diagnosis and identification. Multidimensional scaling, a nonparametric multivariate technique, clearly separates the two species on the basis of pelvic fin length, head length, number of second dorsal fin rays and origin of the lower lateral line relative to the anal fin rays. We provide a revised identification key to the species of *Cryodraco*. From a zoogeographical point of view, *C. antarcticus* has a circum-Antarctic distribution whereas *C. atkinsoni* is largely confined to the East Antarctic Zoogeographic Province.

Introduction

Antarctic icefishes of the notothenioid family Channichthyidae are a unique and important element of the fish fauna of the Southern Ocean. Since these intriguing fish lack haemoglobin and have variable patterns of myoglobin expression in muscle tissues, they have been intensively studied from morphological, physiological, genetic and evolutionary perspectives (Iwami 1985; Cocca et al. 1995; Sidell et al. 1997; Chen et al. 1998; Detrich 2000; Moylan and Sidell 2000; O'Brien and Sidell 2000). Channichthyids are a major component of fish biomass in many shelf areas (Ekau 1990; Eastman and Hubold 1999), and commercial fishing for *Champsocephalus gunnari* began in 1976 (Kock 1992). In addition, members of the genera *Chionobathyscus* and *Cryodraco* sometimes compose a major component of by-catch in longlining for toothfish of the genus *Dissostichus* (Arana and Vega 1999). Despite the interest in channichthyids, the number of species in the family is still uncertain. A widely utilised monograph on fishes of the Southern Ocean recognises 15 species of channichthyids (Iwami and Kock 1990), while other works delineate 16 (Hureau 1985), 18 (Miller 1993) and 20 (Balushkin 2000) species. With three nominal species, the genus *Cryodraco* has been a continuing focus of taxonomic uncertainty.

Cryodraco antarcticus Dollo (1900), the type for the genus, is common and widespread on the Antarctic continental shelf (Iwami and Kock 1990), and its validity is unquestioned.

The taxonomic status of *Cryodraco pappenheimi* Regan (1913), described by Regan from a single specimen collected by Pappenheim (1912), has been problematic. The holotype has been lost and Iwami and Kock (1990) referred this species to the genus *Chionodraco*. Miller (1993) subsequently identified as *Cryodraco pappenheimi* a specimen (USNM 214687) caught off the Palmer Archipelago (Antarctic Peninsula) in 1966. Balushkin (1996), however, notes that this specimen lacks some of the most conspicuous characters of *Cryodraco*, including three lateral lines, and suggests it is more likely allied to the genus *Chaenocephalus*. Miller (1993) maintains that his specimen of *Cryodraco pappenheimi* (210 mm SL) has longer pelvic fins than *Chaenocephalus*. However, there is an ontogenetic decrease

M. La Mesa (✉)
CNR, Istituto di Ricerche sulla Pesca Marittima,
Largo Fiera della Pesca, 60125 Ancona, Italy
E-mail: lamesa@irpem.an.cnr.it
Fax: +39-071-55313

M. Vacchi
ICRAM, Istituto Centrale per la
Ricerca Scientifica e Tecnologica Applicata al Mare,
Via Casalotti 300, 00166 Rome, Italy

T. Iwami
Tokyo Kasei-Gakuin University,
2600 Aihara, Machida 194-0929, Japan

J.T. Eastman
Department of Biomedical Sciences,
College of Osteopathic Medicine,
Ohio University, Athens, OH 45701-2979, USA

in the relative length of the pelvic fins in *Chaenocephalus aceratus*, and this species is not mature until it reaches 475–584 mm TL (Iwami and Kock 1990). While adult *Chaenocephalus aceratus* have short pelvic fins, immature specimens similar in size to Miller's *Cryodraco pappenheimi*, have relatively long pelvic fins. For example, in a 218-mm-SL specimen of *Chaenocephalus aceratus* that we measured, the pelvics were 35% of SL, nearly identical to the 34% obtained by measuring the pelvics in Miller's (1993) illustration of *Cryodraco pappenheimi*. Hence, we agree with Balushkin (1996) that Miller's *Cryodraco pappenheimi* is likely a specimen of *Chaenocephalus*. Therefore, in the absence of the holotype, as well as any additional specimens clearly related to the genus *Cryodraco*, we suggest that *Cryodraco pappenheimi* is a questionable, and probably invalid, species. It will not be further considered in this paper.

The validity of the third species, *Cryodraco atkinsoni* Regan (1914), has also been uncertain. In agreement with Waite (1916), some authors (Norman 1938; Hureau 1985) consider this species as a junior synonym of *Cryodraco antarcticus*. Other studies, based on body morphology and meristic characters, support the validity of *Cryodraco atkinsoni* (Iwami and Abe 1981; Iwami and Kock 1990; Miller 1993; Evseenko 1994; Balushkin 1996, 2000; La Mesa and Vacchi 1997), although some of these workers also indicate that additional research is necessary to clearly define and diagnose the species. All data for *Cryodraco atkinsoni* have been obtained from relatively few museum specimens.

In the past 20 years, a large number of specimens of *Cryodraco* have been collected during Japanese, American and Italian Antarctic research cruises in the western Ross Sea and around the South Shetland Islands (Iwami and Abe 1981, 1982; Iwami 1993; Eastman and Hubold 1999; Vacchi et al. 1999). A few other specimens have been taken in Cooperation Sea (Prydz Bay) and Cosmonaut Sea (Lützow-Holm Bay). By pooling these previously unstudied specimens, we have obtained a suitable data set of morphological and meristic characters that provide additional insight into the taxonomy of the genus *Cryodraco*. In this paper, we (1) summarise meristic and morphometric characters of *Cryodraco antarcticus* and *Cryodraco atkinsoni*, (2) use a multivariate analysis to distinguish the two species, (3) provide a revised identification key, and (4) document new data on geographical distribution.

Materials and methods

Our material consists of 101 specimens of *Cryodraco* collected at several Antarctic localities (Fig. 1). Fifty-eight specimens were taken near the South Shetland Islands (Iwami and Abe 1982); 36 specimens came from the Ross Sea (Iwami and Abe 1981; Eastman and Hubold 1999; Vacchi et al. 1999), and another 6 were collected in the Cooperation and Cosmonaut Seas (Iwami 1993). The holotype of *Cryodraco atkinsoni* from the Ross Sea (Regan 1914, BMNH 1913.12.4.185) is also included in our sample. The references given contain detailed station data for each cruise.

Our specimens are deposited in institutions with abbreviations as follows: BMNH British Museum (Natural History); USNM Smithsonian Institution, National Museum of Natural History; LBTK Laboratory of Biology, Tokyo Kasei Gakuin University; MSNG Museum of Natural History "G. Doria" of Genoa; A Professor Abe's personal collection; B National Museum of Antarctica of Genoa. Catalogue numbers, number of specimens (in parentheses) and localities for the two species are given below.

Cryodraco antarcticus: USNM 366212 (9), southwestern Ross Sea; LBTK 780268, 810100, 810102–810104, 810106, 810210, 810212, 810214–810216, 810238–810239, 810241–810243, 810385, 810427, 810537, 810539, 810542, 810545, 810547, 810549, 810551, 810766, 820164, 820191, 820222–820223, 820292–820293, 820696–820697, 820299, 820315, 820397, 820420–820422, 820433, 820444, 820447–820449, 820486–820487, 820549–820550, 820555, 820667, 820669–820670, 820745, 820758, 823040 and 20010032 (57), South Shetlands; LBTK 822899 (1), Prydz Bay; A 19016′, 19038′–19041′, 19061′ and 19110′ (7), Ross Sea.

Cryodraco atkinsoni: BMNH 1913.12.4.188 (1), Ross Sea; USNM 366213 (5), southwestern Ross Sea; LBTK 820781 (1), South Shetlands; LBTK 822714, 822719, 822900, 822904 (4), Prydz Bay; LBTK 822812 (1), Lützow-Holm Bay; A 19014′ and 19015′ (2), Ross Sea; B 1350 (1) Terra Nova Bay; MSNG 48141 and 48143 (2), Terra Nova Bay.

Following the previous taxonomic identification keys for the genus *Cryodraco* (Hureau 1985; Iwami and Kock 1990; Miller 1993; Balushkin 1996), we selected a series of morphological and

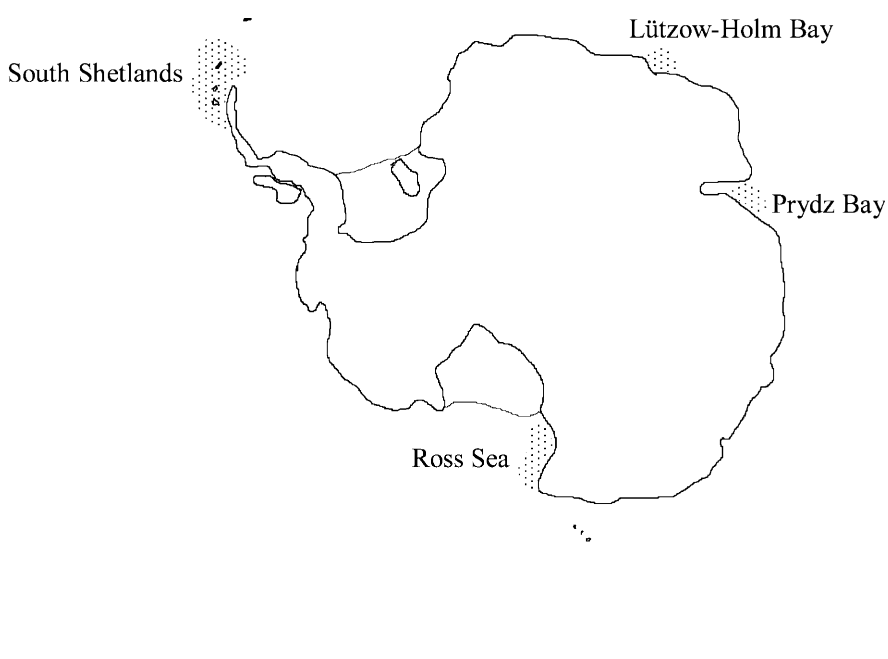

Fig. 1. Map of Antarctica showing sampling sites for *Cryodraco*

meristic characters useful for species diagnosis. These include (with abbreviations and accuracy of measurement): standard length (SL, mm), dorsal (D, spines in the first and rays in the second), anal (A) and pectoral (P) fin rays, head length (HL, 0.1 mm) and snout length (0.1 mm), eye diameter (0.1 mm) and interorbital width (0.1 mm), pectoral fin length (0.1 mm), pelvic fin length (0.1 mm), origin of lower lateral line (LLL) relative to anal-fin ray number, presence/absence of a black blotch on caudal fin and of a rostral spine on the snout. We used needle point dial calipers to obtain morphometric measurements. We counted abdominal and caudal vertebrae on radiographs. We counted the most anterior vertebra bearing a definite hemal spine as the first caudal vertebra, and the last as the single urostylar centrum characteristic of notothenioids. Finally, we sexed most of the specimens macroscopically.

In summarising and comparing meristic and morphometric data for the two species, we utilised descriptive statistics and independent *t*-tests contained in the program SYSTAT (version 5.2.1). One-sample Lilliefors tests, a variant of the Kolmogorov-Smirnov test, indicated about one-half of the characters in Table 1 were not normally distributed. Prior to analysis, we transformed data to natural logarithms (ln). This procedure reduced variance, skewness, kurtosis and the coefficient of variation. The values reported in Table 1 are untransformed; however, levels of significance are for ln-transformed data. Measurements were not independent since we made six meristic counts, three measurements and derived five ratios for each specimen. We therefore used the Bonferroni adjustment to ensure that we accepted a conservative *P*-level as significant.

We also applied a nonparametric multivariate analysis (multidimensional scaling, MDS) to the morphological and meristic data set. We derived a bidimensional plot from a Bray-Curtis coefficient of similarity matrix calculated from standardised data. To determine relevant contributions to the point spatial distribution, we performed an analysis of percentage similarity for each character using a SIMPER routine. Furthermore, we used a one-way statistical analysis (ANOSIM routine) to test the null hypothesis (i.e. no statistical difference between samples). For this purpose, we employed the software package PRIMER (Plymouth Routines In Multivariate Ecological Research) developed at the Plymouth Marine Laboratory (Clarke and Warwick 1994; Carr 1996).

Results

Of the 101 specimens examined, we identified 27 as *Cryodraco atkinsoni* and 74 as *Cryodraco antarcticus*. Figure 2 displays the length-frequency distribution for the two species. Standard length was 164–472 mm for *C. atkinsoni* and 141–472 mm for *Cryodraco antarcticus*, although the mean length was significantly larger in *Cryodraco atkinsoni* (Table 1). The values in Table 1 are a considerable extension of the known range for many meristic and morphometric characters, especially in the case of *Cryodraco atkinsoni*, which has been poorly characterised. Table 1also indicates that, while there are significant differences in some morphometric ratios and fin-ray counts, the two species overlap in all meristic and morphometric characters utilised for identification. On average, *Cryodraco atkinsoni* possesses one less dorsal ray and one more anal ray and pectoral ray than *Cryodraco antarcticus*. However, significant mean differences are of little practical value in separating individuals of the two species when ranges overlap to this extent. Hence the origin of the lower lateral line relative to the anal fin rays emerges as an essential diagnostic character. Based on selected morphological and meristic characters in Table 1 and on the literature (Iwami and Kock 1990; Miller 1993; Balushkin 1996), the taxonomic diagnosis of the two species is as follows.

Cryodraco antarcticus

D II–VI +41–46; A 41–46; P 22–26. Vertebrae (25–29) + (39–44) = 67–70. Head length 29.2–37.9% and pelvic-fin length 22.6–70.4% of SL. Snout length 44.3–54.3%, eye diameter 16.7–23.9% and interorbital width 17.5–25.7% of HL. Origin of lower lateral line above base of 1st–11th anal fin rays. Dark blotch present on posterior margin of caudal fin; rostral spine present on the snout.

Cryodraco atkinsoni

D II–VI +40–46; A 42–46; P 24–26. Vertebrae (25–27) + (41–43) = 67–70. Head length 31.0–34.8% and pelvic-fin length 23.6–61.8% of SL. Snout length 41.5–50.0%, eye diameter 16.1–21.3% and interorbital width 19.6–25.2% of HL. Origin of lower lateral line above base of

Table 1. Morphometric and meristic comparison of *Cryodraco atkinsoni* and *Cryodraco antarcticus*. Numbers of specimens are 27 for *Cryodraco atkinsoni* and 74 for *Cryodraco antarcticus*, with the exception of vertebrae where numbers are 20 and 67, respectively. *P*-level determined by independent *t*-tests on ln-transformed data. *Asterisks* denote significance at the Bonferroni-adjusted *P*-level of $0.05/14 = P < 0.0036$

Character	*C. atkinsoni*[a]	*C. antarcticus*[a]	P
Standard length (SL, mm)	391 (74) 164–472	288 (76) 141–472	< 0.0001*
Head length (HL, mm)	129.6 (24.4) 51.4–153.0	98.1 (30.2) 42.9–168.4	< 0.0001*
Pelvic fin length (VFL, mm)	111.8 (5.2) 101.3–122.0	115.1 (13.4) 95.6–146.4	0.1475
HL as % SL	33.2 (1.1) 31.0–34.8	33.8 (1.8) 29.2–37.9	0.0729
VFL as % SL	30.1 (8.4) 23.6–61.8	42.4 (10.4) 22.6–70.4	< 0.0001*
Snout length as % HL	46.1 (2.0) 41.5–50.0	48.2 (2.1) 44.3–54.3	0.0001*
Eye diameter as % HL	18.9 (1.4) 16.1–21.3	21.4 (2.1) 16.7–23.9	0.0001*
Interorbital width as % HL	22.3 (1.4) 19.6–25.2	21.4 (2.1) 17.5–25.7	0.0048
Dorsal spines (D1)	4.0 (1.0) 2–6	4.2 (0.8) 2–6	0.3095
Dorsal rays (D2)	43.1 (1.4) 40–46	44.2 (1.0) 42–46	0.0005*
Anal rays (A)	44.6 (1.0) 42–46	43.5 (0.8) 41–46	< 0.0001*
Pectoral rays (P)	24.6 (0.6) 24–26	23.8 (1.0) 22–26	< 0.0001*
Total vertebrae	68.2 (0.8) 67–70	68.8 (0.8) 67–70	0.0052
LLL originates above base of A ray	13.8 (1.9) 11–19	4.8 (2.1) 1–11	< 0.0001*

[a]Reported values are mean (SD) with range below

10th–22nd anal fin ray. Dark blotch absent on posterior margin of caudal fin; rostral spine absent on the snout.

Given the extensive overlap in characters between the two species of *Cryodraco*, we employed multidimensional scaling as an additional method of evaluating differences between the species. On the basis of previous studies of the genus (Hureau 1985; Iwami and Kock 1990; Miller 1993; Balushkin 1996; La Mesa and Vacchi 1997), we selected the following 13 characters as relevant for the MDS analysis: 1st dorsal fin spines, 2nd dorsal fin rays, anal fin rays, pectoral fin rays, pelvic fin length, head length, interorbital width, eye diameter, HL in SL, interorbital width in HL, eye diameter in HL, pelvic fin length to HL, origin of lower lateral line relative to anal fin rays.

The MDS plot shows a clear separation of the two species, at least for fish of large size (Fig. 3, points of second and third quadrants), and this is supported by a low value of stress (0.04). Except for three smaller specimens in the fourth quadrant, all specimens of *Cryodraco atkinsoni* cluster in the third quadrant. However, points for *Cryodraco antarcticus* are more scattered, especially those in the first and fourth quadrants (i.e. smaller specimens). With increasing size, variability decreases (with respect to the vertical axis) and larger specimens cluster primarily in the second quadrant. In order to test whether or not the point distribution in the bidimensional plot was linked to sex, we indicated this character on the ordination coordinates. The plot reveals no clear separation of the sexes, thus supporting the interpretation that the species separation within the ordination plot is real and unrelated to sex.

The similarity percentage analysis (SIMPER) allows determination of the relevant contribution to the point spatial distribution of each selected character (Table 2), as well as linkage to the vertical and horizontal axes. As indicated in the MDS plot, the horizontal axis represents head length (or more generally standard length which is strictly related) and shows the most variability. Although head length accounts for about 29% of point distribution, its values largely overlap between the two species. The vertical axis represents a more complex combination of characters (Fig. 3), such as pelvic fin length, 2nd dorsal fin rays and origin of lower lateral line (Table 2), and it separates the larger specimens of the two species (second and fourth quadrants) into two distinct groups.

Based on the point distribution pattern in the two-dimensional plot, a one-way statistical analysis (ANOSIM) allowed us to reject the null hypothesis, indicating a statistically significant difference between the species ($R = 0.275$, $P < 0.1\%$). In the light of our findings, we provide a key to the valid species of *Cryodraco*, revised with respect to the previous studies of Miller (1993) and Balushkin (1996).

1a Rostral spine present on snout. Posterior portion of caudal fin with a conspicuous dark blotch. Number of rays in anal fin is usually the same or less than in the second dorsal fin; occasionally one more than second dorsal. Tubular scales of the lower (anal) lateral line extend forward to 1st–11th anal rays ....*Cryodraco antarcticus* Dollo, 1900 (Fig. 4A)

1b Rostral spine absent on snout. Posterior portion of caudal fin without dark blotch. Number of rays in anal fin is always the same or greater (up to 4 rays) than in the second dorsal fin. Tubular scales of the lower (anal) lateral line extend forward to 10th–22nd anal rays ....*Cryodraco atkinsoni* Regan, 1914 (Fig. 4B)

Although colour and colour pattern are dubious taxonomic characters in many notothenioids, there is usually a distinct difference between the two species of

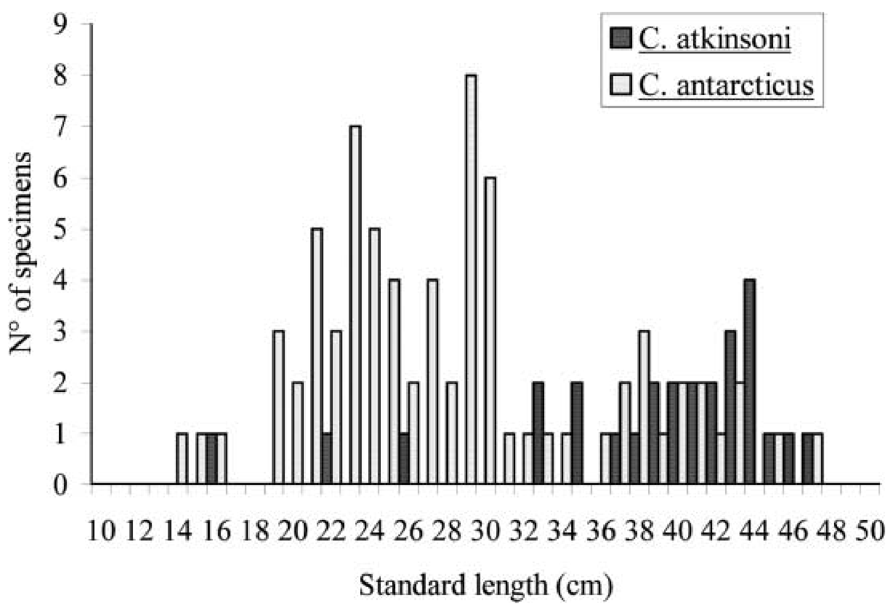

Fig. 2. Length-frequency distribution for *Cryodraco*

Cryodraco in the pattern of dark banding along the trunk, a fact previously noted by other workers (Iwami and Kock 1990; Miller 1993; Balushkin 1996). Based on our experience with both fresh and preserved specimens of *Cryodraco*, this is a readily apparent and useful feature for quickly identifying most specimens of the two species. *Cryodraco antarcticus* has 5–6 relatively thick cross-bars on the trunk whereas *Cryodraco atkinsoni* has 7–8 thinner cross-bars (Fig. 4). Furthermore, specimens of *Cryodraco atkinsoni* from the southwestern Ross Sea (USNM 366213) possess small dark blotches or mottling on the snout, upper jaw, dorsum of head and occiput. These markings are not present in *Cryodraco antarcticus* from the same locality (USNM 366212).

Based on our collections, *Cryodraco atkinsoni* is confined almost exclusively to the East Antarctic Zoogeographic Province, with documented specimens from the Ross, Cooperation and Cosmonaut Seas. The sole exception is a specimen from the South Shetland Islands. *Cryodraco antarcticus*, however, has a circum-Antarctic distribution.

Discussion

Unlike previous taxonomic studies of the genus *Cryodraco* (Iwami and Kock 1990; Miller 1993; Balushkin 1996), our data are derived from a large sample. The importance of sample size in taxonomic research is highlighted by the remarkable difference between our results and those in the literature, specifically overlap in the most essential morphological and meristic characters for the two species. Furthermore, the use of a large number of specimens has expanded the known range for most characters.

The most recent identification key for the species of *Cryodraco* (Balushkin 1996) is in need of revision. In particular, the position of the anal fin origin relative to the second dorsal fin origin is unreliable as a diagnostic character, as has been previously suggested (La Mesa and Vacchi 1997). Similarly, the lower lateral line origin relative to the anal fin rays is partially overlapping between the species, although this character is still considered most important in species diagnosis. The presence or absence of the rostral spine on the snout and the dark blotch on the posterior portion of the caudal fin should resolve any doubt in species identification.

The two-dimensional plot derived from the MDS analysis indicates greater variability in body morphology in *Cryodraco antarcticus* than in *Cryodraco atkinsoni*, at least for those characters we have selected. This is most evident in smaller specimens of *Cryodraco antarcticus*, which show a decrease in variability with ontogeny, at least for pelvic fin length (see the first and fourth quadrants Fig. 3). However, the tight clustering of samples of *Cryodraco atkinsoni* is surprising, and sug-

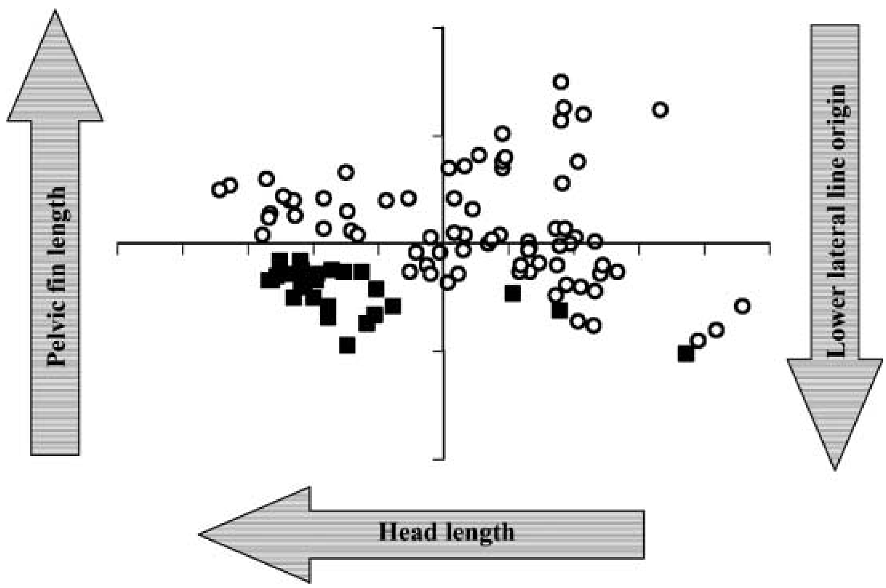

Fig. 3. MDS plot of *Cryodraco* specimens (■ *Cryodraco atkinsoni*; ○ *Cryodraco antarcticus*). *Arrows* represent the most important characters determining point distribution. The *quadrants* are numbered counter clockwise, with the first quadrant at the *upper right*

Table 2. Data from similarity percentage analysis (SIMPER) [*A* average abundance of *Cryodraco atkinsoni*; *B* average abundance of *Cryodraco antarcticus*; *C* average dissimilarity; *D* dissimilarity/SD; *E* contribution (%); *F* cumulative (%)]

Character	A	B	C	D	E	F
Head length	129.60	98.08	3.04	1.59	28.72	28.72
Pelvic fin length	111.83	115.08	2.4	1.63	22.72	51.44
Dorsal rays (D2)	43.07	44.16	0.99	1.49	9.32	60.76
Origin of the LLL	13.85	4.81	0.97	2.84	9.14	69.9
Interorbital width	29.16	21.32	0.92	1.6	8.69	78.59
Anal rays	44.63	43.5	0.82	1.36	7.74	86.33
Eye diameter	24.34	19.76	0.52	1.46	4.87	91.2

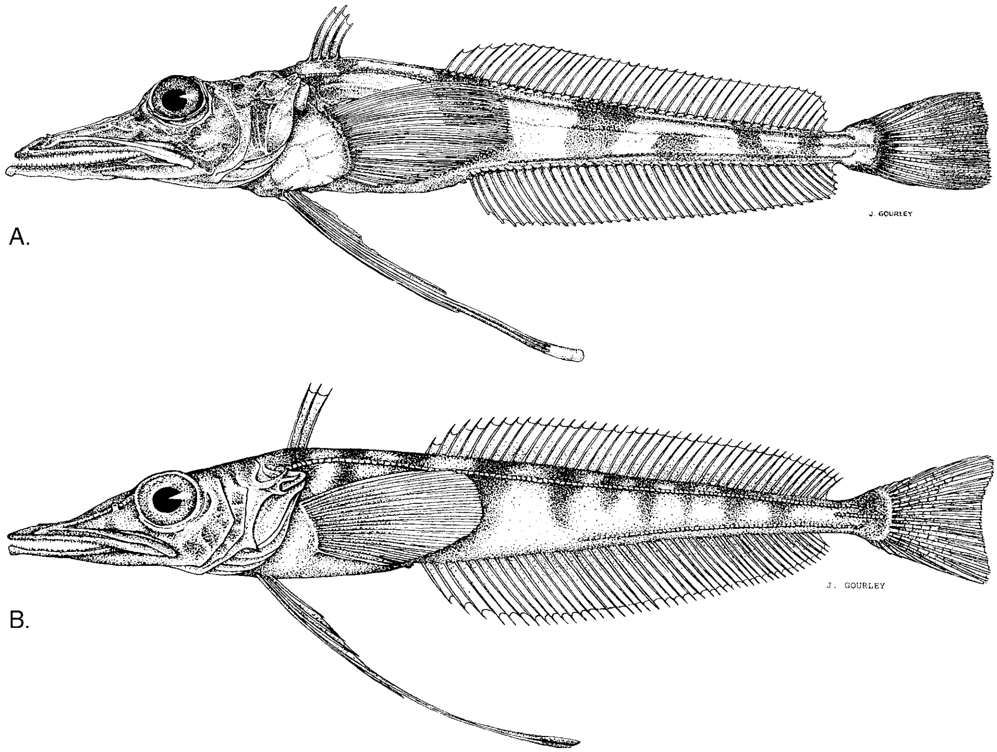

Fig. 4. *Cryodraco antarcticus* (**A**) and *Cryodraco atkinsoni* (**B**) showing some of the key diagnostic features of these species. From Miller (1993), with permission of the author and the Foresta Institute for Ocean and Mountain Studies. Drawings by Josette Gourley

gests a more conservative trend in body morphology. From a zoogeographical perspective, *Cryodraco antarcticus* has a circum-Antarctic distribution whereas *Cryodraco atkinsoni* is largely confined to the East Antarctic Province, with the exception of one specimen caught in the South Shetland Islands. In the Ross Sea, where most of our specimens of *Cryodraco atkinsoni* were collected, the two species are sympatric and live on the shelf to depths of about 350 m.

In conclusion, after examining a large number of specimens, we endorse recognition of *Cryodraco atkinsoni* as a valid species. Given that it is a readily identifiable form and that a scientific name has been available for nearly 90 years, we see no reason for underestimating Antarctic fish diversity. Other workers have also shown some inclination to recognise *Cryodraco atkinsoni* (Iwami and Abe 1981; Iwami and Kock 1990; Miller 1993; Balushkin 1996; La Mesa and Vacchi 1997), but usually with reservations because of small sample sizes or inadequate study. In our large sample, the two species do exhibit substantial overlap in the ranges of morphological and meristic characters and also have partially overlapping geographic distributions. However, within the range of overlapping characters, MDS reveals a suite of characters that separate the two species. Furthermore, supplemental characters, including colour pattern, also contribute to identification of the species.

Unfortunately, fresh tissue was not available from our specimens, but future work should focus on obtaining molecular sequence data for assessment of the genetic variability within *Cryodraco*.

Acknowledgements M.L.M. and M.V. were supported by the Italian National Project of Antarctic Researches (PNRA). J.T.E. was supported by US National Science Foundation grant OPP 94-16870 and by an Ohio University Presidential Research Scholar Award. T.I. was partially supported by the Japan Society for the Promotion of Science, Grant-in-Aid for Scientific Research (C), 08640896 and 12640686.

References

Arana PM, Vega R (1999) Exploratory fishing for *Dissostichus* spp. in the Antarctic region (subareas 48.1, 48.2 and 88.3). CCAMLR Sci 6:1–17

Balushkin AV (1996) Similarity of fish of family Channichthyidae (Notothenioidei, Perciformes), with remarks on the species composition of the family and the description of a new species from the Kerguelen Archipelago. J Ichthyol 36:5–14

Balushkin AV (2000) Morphology, classification, and evolution of notothenioid fishes of the Southern Ocean (Notothenioidei, Perciformes). J Ichthyol 40 [Suppl 1]:74–109

Carr MR (1996) PRIMER User manual. Plymouth Routines In Multivariate Ecological Research. Plymouth Marine Laboratory

Chen WJ, Bonillo C, Lecointre G (1998) Phylogeny of the Channichthyidae (Notothenioidei, Teleostei) based on two mitochondrial genes. In: Prisco G di, Pisano E, Clarke A (eds) Fishes of Antarctica: a biological overview. Springer, Milan, pp 287–298

Clarke KR, Warwick RM (1994) Change in marine communities: an approach to statistical analysis and interpretation. Natural Environment Research Council, UK

Cocca E, Ratnayake-Lecamwasam M, Parker SK, Camardella L, Ciaramella M, Prisco G di, Detrich HW (1995) Genomic remnants of α-globin genes in the hemoglobinless antarctic icefishes. Proc Natl Acad Sci USA 92:1817–1821

Detrich HW (2000) Recent evolution of the hemoglobinless condition of the Antarctic icefishes. In: Prisco G di, Giardina B, Weber RE (eds) Hemoglobin function in vertebrates: molecular

adaptation in extreme and temperate environments. Springer, Milan, pp 39–49
Dollo L (1900) *Cryodraco antarcticus*, poisson abyssal nouveau recueilli par l'Expédition Antarctique Belge (communication préliminaire). Bull Acad R Belg 2:128–137
Eastman JT, Hubold G (1999) The fish fauna of the Ross Sea, Antarctica. Antarct Sci 11:293–304
Ekau W (1990) Demersal fish fauna of the Weddell Sea, Antarctica. Antarct Sci 2:129–137
Evseenko SA (1994) Larval and juvenile fishes from collections made under the ice in the Weddell Sea. J Ichthyol 34:128–133
Hureau JC (1985) Channichthyidae. In: Fischer W, Hureau JC (eds) FAO Species Identification Sheets for Fishery Purposes, Southern Ocean, vol 2. FAO, Rome, pp 261–277
Iwami T (1985) Osteology and relationships of the family Channichthyidae. Mem Natl Inst Polar Res E (36):1–69
Iwami T (1993) Fishes collected during the JARE-34 cruise in 1992–1993. Polar News 57:47–51
Iwami T, Abe T (1981) The collection of the fishes trawled in the Ross Sea. Antarct Rec 71:130–141
Iwami T, Abe T (1982) Notes on the fishes collected during the 1980–81 exploratory bottom trawl fishing off the South Shetland Islands. Mem Natl Inst Polar Res 23:55–63
Iwami T, Kock KH (1990) Channichthyidae. In: Gon O, Hemstra PC (eds) Fishes of the Southern Ocean. J.L.B. Smith Institute of Ichthyology, Grahamstown, pp 381–399
Kock KH (1992) Antarctic fish and fisheries. Cambridge University Press, Cambridge
La Mesa M, Vacchi M (1997) Morphometric analysis of *Cryodraco* specimens (Osteichthyes, Channichthyidae) from Terra Nova Bay, Ross Sea. Cybium 21:363–368
Miller RG (1993) A history and atlas of the fishes of the Antarctic Ocean. Foresta Institute for Ocean and Mountain Studies, Carson City
Moylan TJ, Sidell BD (2000) Concentrations of myoglobin and myoglobin mRNA in heart ventricles from Antarctic fishes. J Exp Biol 203:1277–1286
Norman JR (1938) Coast fishes. Part III. The Antarctic Zone. Discovery Rep 18:1–104
O'Brien KM, Sidell BD (2000) The interplay among cardiac ultrastructure, metabolism and the expression of oxygen-binding proteins in Antarctic fishes. J Exp Biol 203:1287–1297
Pappenheim P (1912) Die Fische der deutschen Südpolar-Expedition 1901–1903. I. Die Fische der Antarktis und Subantarktis. Dtsch Südpolar Exped Zool 13:160–182
Regan CT (1913) The Antarctic fishes of the Scottish National Antarctic Expedition. Trans R Soc Edinburgh 49:229–292
Regan CT (1914) Fishes. British Antarctic ("Terra Nova") Expedition 1910, Natural History Report. Zoology 1:1–54
Sidell BD, Vayda ME, Small DJ, Moylan TJ, Londraville RL, Yuan ML, Rodnick KJ, Eppley ZA, Costello L (1997) Variable expression of myoglobin among the hemoglobinless Antarctic fishes. Proc Natl Acad Sci USA 94:3420–3424
Vacchi M, La Mesa M, Greco S (1999) The coastal fish fauna of Terra Nova Bay, Ross Sea (Antarctica). In: Faranda FM, Guglielmo L, Ianora A (eds) Ross Sea ecology. Italiantartide Expeditions (1987–1995). Springer, Milan, pp 457–468
Waite ER (1916) Fishes. Australasian Antarctic Expedition 1911–1914. Sci Rep Ser C Zool Bot 3:1–92