

Joseph T. Eastman · Richard R. Eakin

Mental barbel and meristic variation in the Antarctic notothenioid fish *Dolloidraco longedorsalis* (Perciformes: Artedidraconidae) from the Ross Sea

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Abstract A collection of 58 specimens of *Dolloidraco longedorsalis* from the southwestern Ross Sea was studied for intraspecific variation in the number of second dorsal and anal rays, number of vertebrae, and length and shape of the mental barbel – a key diagnostic and taxonomic character in this family. Ranges for meristics are compact and extend documented values to 13 for anal rays and 37 for vertebrae. There is a nearly twofold difference in the relative length of the mental barbel. There are no significant differences between the sexes in any meristic or morphometric feature. The terminal expansion of the barbel exhibits four types, documented with illustrations and histology: typical expanded form (43%), not expanded or tapered (33%), slightly expanded (22%), and large expansion (2%). There is no relationship between absolute and relative barbel length and sex or barbel type and sex. There is no relationship between barbel type and size of the specimen. Twenty-five percent of specimens have the epidermis of the terminal expansion arranged as broad ridges or mounds. The mental barbel of *D. longedorsalis* is therefore individually variable with no evidence of sexual dimorphism, and the type of barbel does not vary ontogenetically. Histological analysis of the barbel reveals that the terminal expansion consists of a thick epidermis and that dermal papillae are responsible for the pattern of surface projections sometimes present. The epidermis near the tip of the barbel is twofold

thicker in specimens with a terminal expansion. The distal morphology of the barbel, whether straight or expanded, probably has little functional significance. The barbel is richly supplied with nerves and blood vessels and the core consists of pseudocartilage. The barbel is probably a somatosensory organ.

Introduction

Five endemic families of the perciform suborder Notothenioidei dominate the fish fauna of Antarctic waters. The 96 species of Antarctic notothenioids include 4 genera and 25 species of plunderfishes of the family Artedidraconidae (Eastman and Eakin 2000). In spite of their speciosity, descriptions of most artedidraconids are based on small samples and little is known about the biology of many species (Eakin 1990). Consequently, there are limited data on intraspecific variation, especially variation in the mental barbel – an essential diagnostic and taxonomic character in this family. The function of the barbel, typically held at about 45° from the horizontal, is not completely understood. It lacks taste buds and behavioural evidence suggests that it serves as both an attractant lure and a somatosensory (tactile) device in *Histiodraco velifer* (Janssen et al. 1993). However, other experiments on *H. velifer* and on *Pogonophryne marmorata* do not support its use as a lure but do indicate that it provides tactile input on the presence and position of prey (Iwami et al. 1996).

On the basis of six specimens collected in Marguerite Bay, Roule (1913) described and illustrated (Roule et al. 1913) *Dolloidraco longedorsalis* (Fig. 1) as a new genus and species of artedidraconid. *Dolloidraco* has subsequently been found to be the most abundant artedidraconid at depths >400 m in high latitudes of both the Weddell Sea (Ekau 1990) and the Ross Sea (Eastman and Hubold 1999). Unlike most other artedidraconids, therefore, adequate numbers of *Dolloidraco* are available for the study of intraspecific variation. *Dolloidraco* has

J.T. Eastman (✉)
Department of Biomedical Sciences,
College of Osteopathic Medicine,
Ohio University, Athens,
OH 45701-2979, USA
E-mail: eastman@ohiou.edu
Tel.: +1-740-5932350
Fax: +1-740-5972778

R.R. Eakin
Department of Life Sciences,
University of New England/Westbrook College Campus,
Portland, ME 04103-2670, USA

long been cited as exhibiting variation in barbel morphology (Waite 1916; Norman 1938; DeWitt and Tyler 1960; Eakin 1990; Miller 1993), with a straight or slightly tapered barbel (Figs. 1, 2B) and a barbel with a round terminal expansion (Fig. 2A) as the most com-

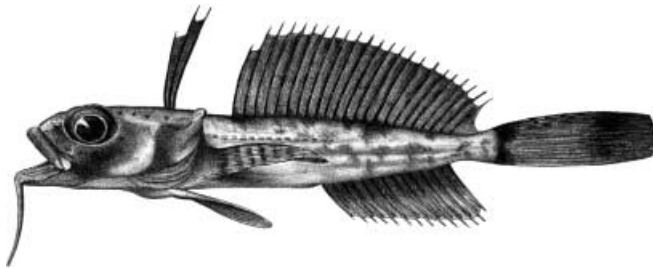


Fig. 1 *Dolloidraco longedorsalis* from Roule et al. (1913), a specimen from the type series. This specimen has a tapered barbel lacking a terminal expansion, the second most frequent type of barbel in our sample

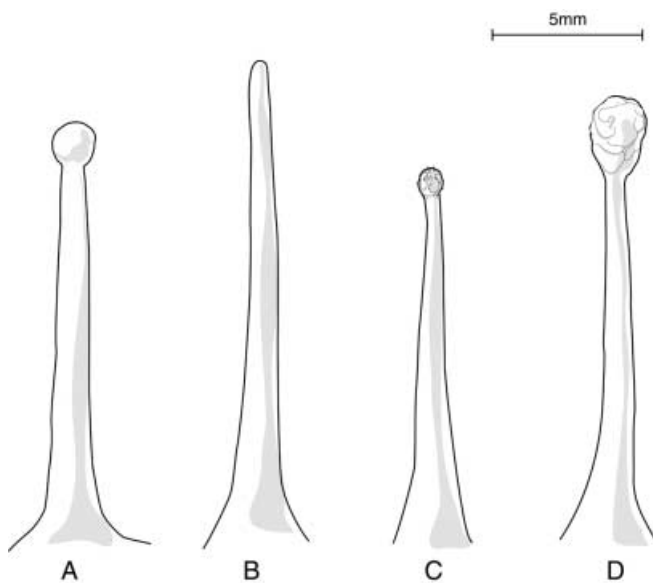


Fig. 2 Camera lucida drawings demonstrating the range of variation in the mental barbels of *Dolloidraco longedorsalis* from the Ross Sea, arranged from most (A) to least (D) common type. **A** Expanded (43%); **B** not expanded or tapered (33%); **C** slight expansion (22%), with skin of expansion atypical in having both ridges and small papillae; **D** large expansion (2%), with skin of expansion also unusual in having a well-developed pattern of ridges and furrows. All are dorsal views of the extended barbel drawn at the same magnification

Table 1 Number of specimens and depth distribution by station for 63 specimens of *Dolloidraco longedorsalis* collected by bottom trawls during cruises 96-6 and 97-9 of the RV *Nathaniel B. Palmer* in the southwestern Ross Sea

Station no.	65	20	30	119 ^a	34	87 ^a
Date	3 Jan 98	24 Dec 97	27 Dec 97	8 Jan 97	28 Dec 97	2 Jan 97
Latitude (S)	77°15'	76°30'	76°16'	77°19'	75°04'	76°00'
Longitude (E)	173°59'	166°17'	165°16'	165°41'	165°10'	171°09'
Depth (m)	530	663	737	910	1191	? ^b
	1	33	1	20	5	3

^aCollected during cruise 96-6

^bMidwater trawl inadvertently hit bottom at unknown depth and captured these specimens

mon forms. It is possible that this may reflect sexual dimorphism (Norman 1938; DeWitt and Tyler 1960; Eakin 1990) as another artedidraconid, *Artedidraaco mirus*, has a sexually dimorphic barbel (Lönnerberg 1905; Norman 1938). There are no taxonomic uncertainties within the monotypic genus *Dolloidraco*, but documentation of the magnitude and nature of barbel variation is relevant for gauging the degree of possible variation among the numerous artedidraconids for which there is no information on barbel variability. Thus, for a sample of 58 specimens of *Dolloidraco*, we: (1) present basic meristic data; (2) give measurements for the barbel; (3) document intraspecific variation in barbel morphology as related to sex and size of specimens, and (4) describe the histology of the barbel.

Materials and methods

Collection of specimens

We collected specimens at high-latitude stations in the southwestern Ross Sea during bottom trawling on cruises 96-6 (11 December 1996 to 8 January 1997) and 97-9 (20 December 1997 to 10 January 1998) of the RV *Nathaniel B. Palmer*. We used a 9.1-m-long, 7.6-m effective width, Marinovich Gulf Coast-style flat trawl, a type of otter trawl. We trawled at a speed of 2.0–3.0 knots for 0.5–1.0 h. Bottom temperature varied from –1.5 to –1.9°C at the stations. Of the 63 specimens collected on these cruises, 58 were available for our study (Table 1). These were deposited as two lots in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA under catalogue numbers USNM 364345 (cruise NBP 96-6) and USNM 364346 (cruise NBP 97-9).

Morphological methods

We measured standard length (SL) and mental barbel length (MBL) and derived the proportion MBL as % of SL. Specimens were sexed by inspection of the gonads under magnification. With the aid of magnification, we obtained meristic counts from left lateral radiographs of all specimens.

Histological techniques

Aboard ship, we preserved most specimens of *Dolloidraco* by immersion in 10% formalin; others were fixed by transcardial perfusion of Bouin's fixative. Although the fish were preserved immediately after capture, the epidermis of some barbels was abraded when fish tumbled inside the trawl with hard-bodied invertebrates and rocks from the substrate. We removed nine barbels from both perfused and immersion-fixed specimens and these barbels were embedded in paraffin according to standard procedures. We cut transverse and longitudinal sections at a thickness of 7 µm. We stained sections with the hematoxylin and phloxine,

periodic acid-Schiff (PAS) procedure including Harris hematoxylin with glacial acetic acid, PAS-alcian blue at pH 2.5, alcian blue at pH 1.0, 0.2% aqueous toluidine blue, Gomori's one-step trichrome, picro-ponceau, Weigert's elastic stain or Bodian's Protargol for 28 h at 50°C.

Statistical analysis

To evaluate the influence of sex on meristic counts and morphometric measurements, we performed independent *t*-tests, with sex as the grouping variable, on all meristic and morphometric features in Table 2. We also used contingency tables to summarise and evaluate categorical data (Table 3). In this analysis we treated sex, size (SL) intervals and barbel types as categorical variables. We assigned specimens to large, medium and small size intervals on the basis of ± 1 SD above or below the mean SL (mean = 78.3 mm SL; large specimens ≥ 89 mm SL; small specimens ≤ 67 mm SL). We also assigned specimens to one of four barbel types based on the appearance of the terminal expansion of the barbel. We used the Pearson chi-square as a test of association among categorical variables. In all cases the null hypothesis was that there was no association. We employed the software program SYSTAT (5.2.1) for statistical analyses.

Results and discussion

Meristics and morphometrics

Table 2 summarises meristic and morphometric data for *Dolloidraco*. These data represent an expansion of the

reported ranges (Eakin 1990; Miller 1993) of anal rays to 13 and of vertebrae to 37. As judged by our sample, the Ross Sea population exhibited a compact distribution of these meristic elements discernible in a lateral radiograph. The number of vertebrae encompassed a range of 3 (35–37), with the coefficient of variation (1.51%) similar to those for vertebral counts of other Ross Sea

Table 3 Contingency tables of sex and specimen size intervals (rows) by barbel type (columns) for *Dolloidraco longedorsalis*. Pearson chi-square is test statistic for association

	Barbel type				Totals (%)
	Expanded (typical)	Not expanded (tapered)	Slight expansion	Large expansion	
Sex					
Male	13	7	5	0	25 (43)
Female	12	12	8	1	33 (57)
Totals (%)	25 (43)	19 (33)	13 (22)	1 (2)	58 (100)
$\chi^2 = 1.98, df = 3, P = 0.58, ns$					
Size (SL) interval					
Large	4	4	3	0	11 (19)
Medium	16	12	8	1	37 (64)
Small	5	3	2	0	10 (17)
Totals (%)	25 (43)	19 (33)	13 (22)	1 (2)	58 (100)
$\chi^2 = 1.01, df = 6, P = 0.98, ns$					

Table 2 Meristic and morphometric data for specimens of *Dolloidraco longedorsalis* from the southwestern Ross Sea with sample separated by sex. *P*-level determined by independent *t*-tests

Feature	Total sample	Males	Females	<i>P</i>
Standard length (SL, mm)				
Mean	78.3	78.5	78.2	0.912, ns
SD	10.8	8.8	12.2	
<i>N</i>	58	25	33	
Range	48.0–96.0			
Second dorsal rays				0.527, ns
Mean	22.6	22.6	22.7	
SD	0.6	0.6	0.7	
<i>N</i>	58	25	33	
Anal rays				0.460, ns
Mean	14.8	14.8	14.7	
SD	0.7	0.7	0.8	
<i>N</i>	58	25	33	
Range	13–16			
Vertebrae				0.610, ns
Mean	35.5	35.6	35.5	
SD	0.5	0.6	0.5	
<i>N</i>	58	25	33	
Range	35–37			
Mental barbel length (MBL, mm)				0.467, ns
Mean	12.3	12.1	12.5	
SD	2.0	1.8	2.2	
<i>N</i>	56	25	31	
Range	8.4–17.0			
MBL (% SL)				0.233, ns
Mean	15.9	15.5	16.2	
SD	2.2	2.2	2.1	
<i>N</i>	56	25	31	
Range	12.4–21.0			

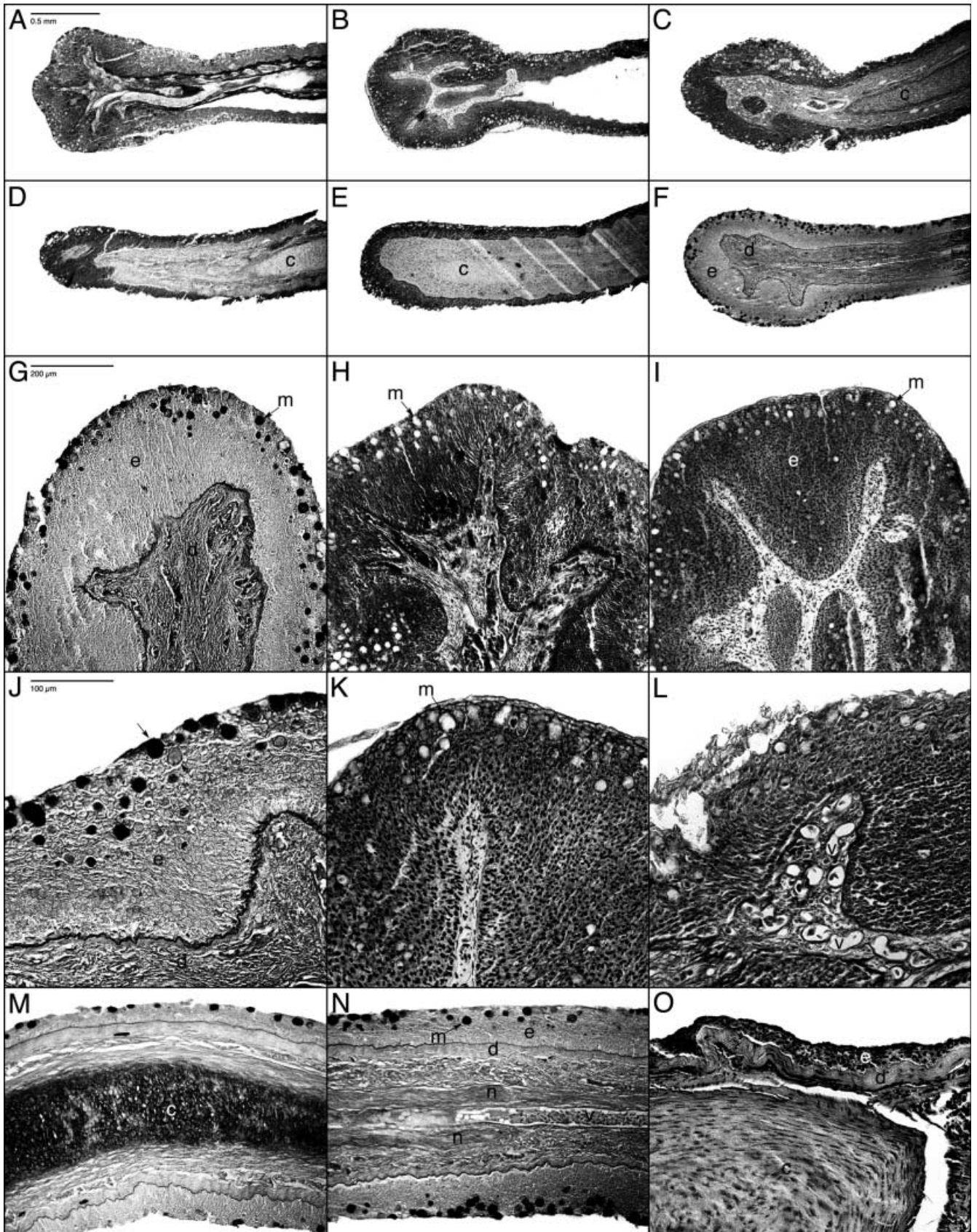




Fig. 3A–O Barbel histology of *Dolloidraco longedorsalis*. **A–C** Low magnification views of barbels with expanded tips, also showing general disposition of epidermis and dermis. **D–E** Low magnification view of barbels with unexpanded tips. **F** Low magnification view of barbel with slightly expanded tip, with superficial epidermis showing distribution of darkly stained mucous cells. **G–I** Epidermis and dermal papillae in barbels with slightly expanded (**G**) and expanded (**H–I**) tips. Ridging of surface epidermis superficial to dermal papilla seen in **H**. **J–L** High magnification views of portion of terminal expansion showing details of epidermis and dermal papillae. Two types of mucous cells (*arrows*) evident in **J** as is dark-staining basement membrane between epidermis and dermis; nuclear staining in **K** indicates extensive cell layers in epidermis; patent blood vessels are obvious in dermal papilla of perfused specimen (**L**). **M–O** Stalk of barbel with and without pseudocartilaginous core. **M** and **N** are longitudinal sections taken proximally (**M**) and distally (**N**) along length of stalk; ground substance of cartilage matrix stains darkly in **M**; cross section (**O**) shows concentrically arranged fibers of matrix and numerous cells (*c* core of barbel; *d* dermis; *e* epidermis; *m* mucous cell; *n* nerve; *v* blood vessel). Stains: **A** picro-ponceau; **B, E, I, K** Bodian's Protargol; **C, D, O** hematoxylin and phloxine; **F, G, J, M, N** periodic acid-Schiff-alcian blue at pH 2.5; **L** Gomori's trichrome. Magnifications: **A–F** ×25; **G–I, M, N** ×75; **J–L, O** ×150

notothenioids (Eastman 1983). Ranges for abdominal and caudal vertebrae in *Dolloidraco* were 13–14 and 21–24, respectively.

With a value of 1.3, the sex ratio of this sample of 33 females and 25 males was not significantly different from unity ($\chi^2 = 0.84$, $df = 1$, $P = 0.359$). Independent *t*-tests indicated no significant differences between the sexes in any of the meristic or morphometric features in Table 2. However, there was nearly a twofold difference in the relative length of the barbel (Table 2).

Barbel types

There was considerable variation in the appearance of the terminal expansion of the mental barbel, and Fig. 2 depicts the four types encountered in our sample. The two most common types, expanded (Fig. 2A) and not expanded (Figs. 1, 2B), accounted for 76% of our sample. These types are based on the relative size of the terminal expansion, not on the appearance of the skin of the expansion. Twenty-five percent of our specimens showed some relief on the skin surface of the terminal expansion, usually a few slight protrusions or knobs (Fig. 3A, H) or a pattern of broad ridges and shallow furrows (Fig. 2C, D). An occasional specimen also had small conical papillae (Fig. 2C). Again we emphasise that size of the terminal expansion, not the pattern of the epidermis, was the basis for our recognition of barbel types.

When the specimens were grouped by sex or by SL into three size intervals (Table 3), Pearson chi-square tests indicated no significant differences for association with mental barbel type. Thus there was no relationship between absolute and relative barbel length and sex (Table 2) or barbel type and sex (Table 3). Nor

was there any relationship between barbel type and size of the specimen (Table 3), indicating that the type of barbel does not vary ontogenetically within our sample ranging from 48 to 96 mm SL (or 50–92% of maximum SL for this species – Eakin 1990). The surface pattern of the epidermis already mentioned was also unrelated to sex and size. We therefore conclude that the mental barbel of *Dolloidraco* is individually variable.

Barbel histology

Figure 3 illustrates the organisation and histology of the barbel of *Dolloidraco*. The epidermis of the barbel consisted of a stratified squamous epithelium that was 200–400 μm thick in barbels with typical terminal expansions (Figs. 2A, 3A–C, H, I, K) and 100–200 μm thick in barbels without terminal expansions (Figs. 2B, 3D, E). The epidermis thinned to 25–50 μm along the stalk of the barbel (Fig. 3M–O). The superficial epidermis contained numerous mucous cells (Fig. 3F, G, J) and staining properties indicated that these cells were of two types (Fig. 3J).

A relatively dense dermis, especially prominent along the stalk (Fig. 3N), was located beneath the epidermis. Less dense dermal or hypodermal connective tissue, containing large nerves and blood vessels, was situated more centrally in the stalk (Fig. 3N) and terminal expansion (Fig. 3G–I). In the stalk these large nerves and vessels were located lateral to the core of the barbel (Fig. 3N) and subsequently branched into small nerves and vessels within dermal papillae near the tip of the barbel. Nerves could not be demonstrated in the epidermis with Bodian's Protargol stain. In a perfused specimen (Fig. 3L), blood vessels in the dermal papillae measured 13–25 μm . The core of the barbel was chondroid or pseudocartilage (Fig. 3C–E, M, O), a typical component in barbels of fish (Harder 1975). The ground substance of the cartilage matrix showed a positive PAS reaction (Fig. 3M). In some areas the matrix was fibrous with numerous cells (Fig. 3O). We found no histological evidence of scarring or damage to the barbel as might occur during feeding.

The ridges and furrows on the skin on the terminal expansion of *Dolloidraco* may reflect the degree of development of the dermal papillae. In mammals, the dermis is known to play an important role in determining the characteristics of the overlying epidermis (Stenn 1988). When well developed, the papillae caused ridges, folds or protrusions on the surface of the epidermis in *Dolloidraco* (Figs. 2C, D, 3A, B, H, I, K). Occasionally, these projections were small conical papillae (Fig. 2C). Dermal papillae, however, did not invariably produce surface relief on the epidermis (Fig. 3F, G), and we suspect this surface relief is functionally insignificant.

Conclusion

Although barbel variability in *Dolloidraco* has long been recognised (Roule 1913; Waite 1916; Norman 1938), it has never been quantified or histologically documented as in our study. Does this variability have functional or adaptive significance? This is difficult to answer in the absence of experiments or direct observation of feeding behaviour. *Dolloidraco* are probably sit-and-wait predators and their diet consists predominantly of polychaetes, with gammaridean amphipods and isopods as less important food sources (Wyanski and Targett 1981; Schwarzbach 1988; Olaso et al. 2000). With a preferred depth range of 400–1,200 m, *Dolloidraco* likely supplement vision with mechanosensory and tactile information. It is possible that the long, well-developed barbel of *Dolloidraco* extends trigeminal somatosensation, by 12–21% of body length, into the water column in front of the mouth. In this regard the distal morphology of the barbel, whether straight, tapered or expanded to a greater or lesser degree, probably has little functional significance. Intraspecific variability is therefore the norm for the barbel of *Dolloidraco*, and it is likely that other artedidraconid species exhibit variation of at least this magnitude. This should be borne in mind when taxonomic keys are constructed for, or used in the identification of, artedidraconids.

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