# Development of the gut in the South African cyprinid fish *Barbus aeneus* (Burchell)

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In *Barbus aeneus*, an omnivorous cyprinid, the pattern of coiling of the gut is well established at a fork length of 60 mm, when five sections can be distinguished, the third and fourth forming the ascending and returning arms of a loop recurved upon itself. The ratio of the gut length to fish length increases in larger fish, with the greatest increase occurring in the looped section. At lengths above 400 mm a second loop begins to develop at the apex of the primary loop. The related piscivorous *B. kimberleyensis*, cannot readily be distinguished from *B. aeneus* on external characters below a fork length of 90 mm. The pattern of coiling of the gut is less complex than that in *B. aeneus* and this appears to offer a method of distinguishing between individuals of the two species at lengths from 35 mm.

*S. Afr. J. Zool.* 1986, 21: 165 – 169

In *Barbus aeneus*, 'n omnivoor van die familie Cyprinidae, is die kronkelpatroon van die spysverteringskanaal by 'n vurklengte van 60 mm reeds gevestig. Vyf afdelings kan onderskei word waarvan die derde en vierde gedeeltes die stygende en terugkerende arms van 'n lus wat op homself teruggevou is, vorm. Die verhouding van spysverteringskanaallengte tot vislengte neem toe in groter vis en hierdie toename kom in die gelusde deel voor. Teen lengtes bo 400 mm begin 'n tweede lus by die punt van die primêre lus vorm. Die verwante visvretende *B. kimberleyensis* kan by vurklengtes onder 90 mm nie geredelik op grond van eksterne kenmerke van *B. aeneus* onderskei word nie. Die kronkelpatroon van die spysverteringskanaal is egter minder kompleks as dié van *B. aeneus* en dit bied 'n moontlike metode om vanaf lengtes van 35 mm tussen indiwidue van die twee spesies te onderskei.

*S.-Afr. Tydskr. Dierk.* 1986, 21: 165 – 169

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Received 28 March 1984; accepted 26 November 1985

In dietary studies of fish it is usual to examine and evaluate the contents of the stomach. In cyprinid fishes there is no true stomach, the bile duct entering the alimentary canal shortly after the latter enters the coelomic cavity. Although there is no sphincter delimiting the foregut and controlling the passage of food from the stomach, the straight anterior portion of the intestine is often somewhat expanded and muscular and is termed the 'pseudogaster' (Harder 1975). Posterior to this the gut is more or less coiled, the degree of coiling being related to the diet. In carnivorous species the gut is short and simple. In omnivorous species it is longer and in vegetarian species it is very long and shows a complex system of loops (Al-Hussaini 1949).

Kruger & Mulder (1973), in a note on the relationship between diet and the ratio of gut length to fork length in South African cyprinid fish, found that in the omnivorous *Barbus aeneus* (Burchell), then known as *B. holubi* Steindachner (Hocutt & Skelton 1983), vegetable material forms an increasing proportion of the diet after the fish attain a fork length of about 200 mm, and noted that the ratio of gut length to fork length increased as the fish grew. In *B. kimberleyensis* Gilchrist and Thompson, a carnivore, the gut was relatively shorter than in *B. aeneus*. However, Kruger & Mulder (1973) did not study the morphology or histology of the gut of either species.

The ontogeny of gut morphology in a number of Asian cyprinids was documented by Kafuku (1975) who found a variety of patterns of coiling. In a study of the diet of the smallmouth yellowfish, *B. aeneus*, in the P.K. le Roux Dam, a large impoundment on the Orange River in South Africa, the gut contents of 682 individuals ranging in fork length from 10 to 547 mm (Table 1) were examined (Eccles 1986). This provided an opportunity to study changes in the pattern of coiling and in the relative proportion of the different gut sections during growth and thus to establish a morphological basis for studies on diet of the fish. Unfortunately the gut sections were destroyed by the subsequent removal of their contents, making complementary histomorphological studies impracticable.

## Material and Methods

Many of the fish used in the dietary studies were collected during routine quarterly surveys of the dam by officers of the Cape Department of Nature and Environmental Conservation who measured the fork length. Therefore this measure was used in the present work, rather than standard length which is more usual in morphological and taxonomic studies. In addition to the fish taken during the survey, many were

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**Table 1** Length frequency distribution of a sample of 682 *B. aeneus*

| Length (mm) | Number |
|---|---|
| 10 – 25 | 12 |
| 26 – 50 | 16 |
| 51 – 75 | 13 |
| 76 – 100 | 9 |
| 101 – 125 | 18 |
| 126 – 150 | 39 |
| 151 – 200 | 219 |
| 201 – 250 | 206 |
| 251 – 300 | 93 |
| 301 – 350 | 16 |
| 351 – 400 | 26 |
| 401 – 450 | 12 |
| 451 – 500 | 2 |
| 501 – 550 | 1 |
| Total | 682 |

caught specifically for the dietary studies and in most of these both standard length and fork length were measured.

The smallest fish were preserved in formalin and dissected in the laboratory. In larger fish the gut was severed where it entered and left the coelomic cavity and was immediately preserved in 10% formalin. In the laboratory the liver, spleen, gall bladder, fat and mesenteries were dissected away.

The gut was divided, on the basis of consistent points of inflection, into sections which were measured. In the smallest fish the sections were almost straight but in fish longer than about 30 mm a consistent pattern of coiling became established and five sections were delimited (Figure 1). The first of these was the pseudogaster (P) which was almost straight. At (A) the gut narrowed and turned through almost 180° to run forward for about half the length of the pseudogaster. It then curved mesially and again, at (B), anteriorly, leading into a loop. This recoiled upon itself at (C) which came to lie near (B), running back parallel to itself until (D), which lay in the mesentery between (B) and (C). From here it curved gently, first dorsally and then posteriorly, to end at the vent.

In the smallest fish, before coiling became established, the gut sections were measured with calipers, the values being summed to derive the total length. In larger fish, where coiling had developed, the gut was straightened along a ruler to measure the total length and was then cut into sections at (A), (B), (C) and (D) and the sections were individually measured. Because of stiffening from preservation, and because of the presence of sharp bends, the measured total gut length rarely agreed exactly with the sum of the lengths of the sections. This error was, however, minor in relation to the total range of variability.

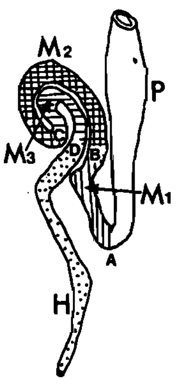

**Figure 1** Dissected alimentary canal of *B. aeneus* 63 mm in fork length, indicating the five sections and points of inflection mentioned in the text. In consideration of the relative lengths of the sections, Section P is the pseudogaster, Sections M1 – M3 constitute the mid-gut and Section H is the hind gut.

The sections used in the analysis of relative lengths were:

| | | |
|---|---|---|
| Foregut | Pseudogaster | Anterior end to A |
| Mid-gut | Section 2 (M 1) | A to B |
| | Section 3 (M 2) | B to C |
| | Section 4 (M 3) | C to D |
| | Section 4a | Develops by involution at C, absent in fish shorter than 400 mm. |
| Hind gut | Section 5 | D to vent. |

## Results

### Changes in gross morphology

During growth the ratio of gut length to fork length and the degree of involution of the gut increase (Figures 2, A – L; 3, M – Q). In fish of fork length less than 12 mm the gut is a straight tube, less than 50% as long as the fork length (A) but in fish of about 14 mm an inflection begins to develop some 40% of the distance along the gut (B). In 20-mm fish the gut has a simple 'N' shape, the posterior portion of the gut being displaced to the left. The middle section is much shorter than the pseudogaster, itself shorter than the posterior section, while the length of the whole gut does not exceed 60% of the fish length (C, D).

The central portion elongates progressively relative to the pseudogaster and hind gut. At a length of about 25 mm a second inflection develops at the anterior end of the hind gut (E, F) and a loop begins to form. This is well developed in fish of 60 mm (G – L) at which size the gut is approximately as long as the fish. The loop extends dorsally, later recurving and coiling posteriorly and then ventrally until it overlies the pseudogaster and the first section of the mid-gut (M – O). The posterior part of the central section becomes increasingly sinuous, being displaced by the developing loop which continues to increase in length in relation to the rest of the gut and comes to cover the whole ventral surface of the visceral mass (Q) and to extend to the right side of the fish. In fish of more than 400 mm, when the gut length is about 1,75 times the fork length, a second loop begins to develop near the apex of the primary loop, lying in the mesentery between the third and fourth sections.

### Changes in relative lengths

Kruger & Mulder (1973) gave a linear relationship between gut length and fork length in *B. aeneus*, but a logarithmic relationship provides a better fit for the present data ($r^2$ for linear is 0,79: for log/log 0,93).

During growth the ratio between the fork length and the length of the pseudogaster changes relatively little, but the ratios between the lengths of the other sections and fork length increase progressively (Figure 4). There was considerable variability in the data, which is reflected in the departure from unity of the value of $r^2$, but a consistent pattern existed. The greatest change was found in the mid-gut, which is not distinguishable in fish below about 14 mm in length. This section grows particularly rapidly in fish between 14 and 30 mm. At the latter point there is a marked inflection in the curve for the ratio of mid-gut length to fork length, although this section still shows the highest rate of increase in length.

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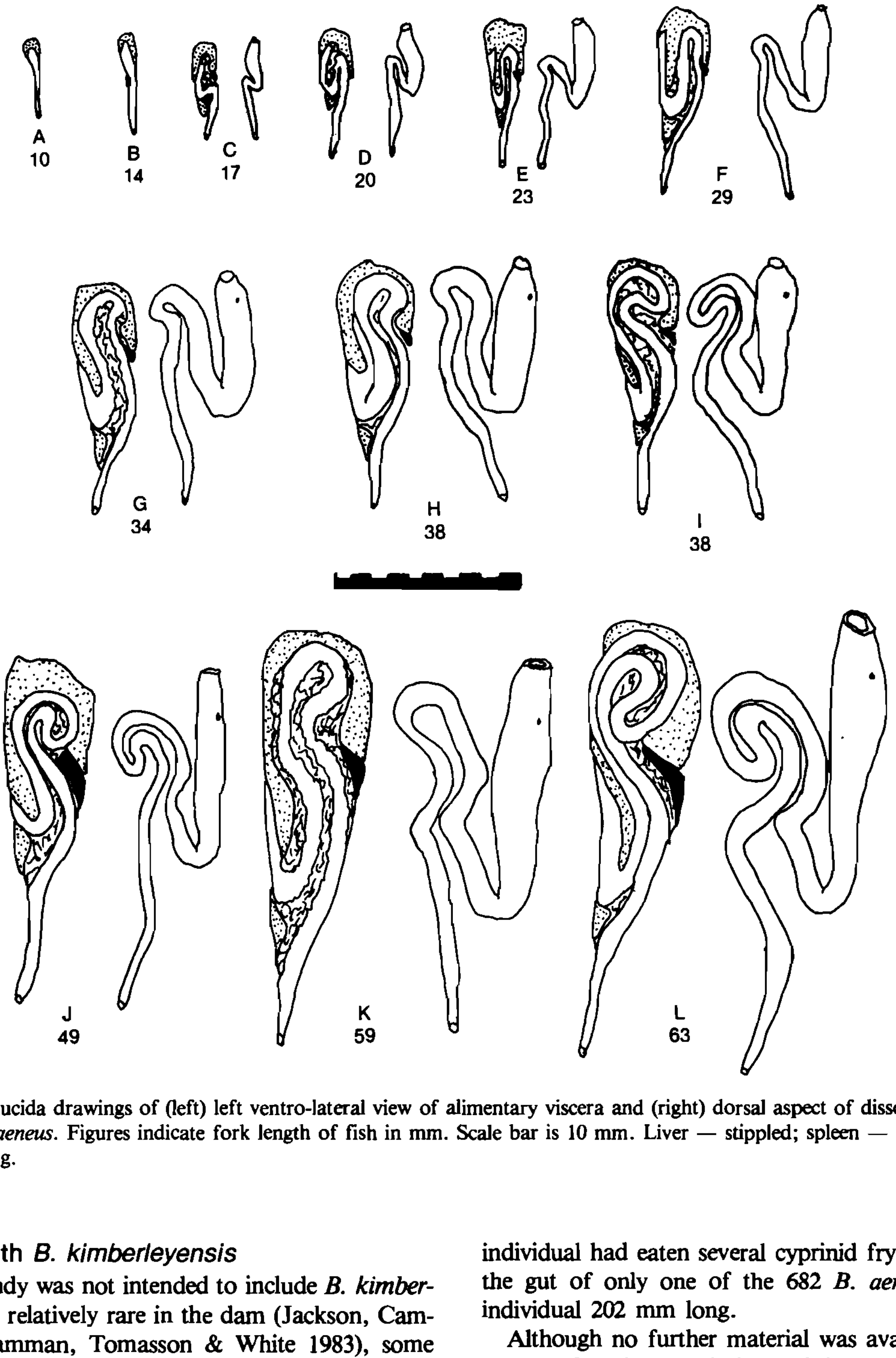

**Figure 2** Camera lucida drawings of (left) left ventro-lateral view of alimentary viscera and (right) dorsal aspect of dissected alimentary canal of juvenile *Barbus aeneus*. Figures indicate fork length of fish in mm. Scale bar is 10 mm. Liver — stippled; spleen — solid shading, and fat — irregular hatching.

### Comparison with *B. kimberleyensis*

Although this study was not intended to include *B. kimberleyensis*, which is relatively rare in the dam (Jackson, Cambray, Eccles, Hamman, Tomasson & White 1983), some incidental information was available. The two species cannot be distinguished on the basis of external morphology below a fork length of 90 mm. Fourteen sub-adults and one adult of *B. kimberleyensis* were examined. The gut is shorter than in *B. aeneus* of a similar size and even in the largest individuals examined (350 mm F.L.) the mid-gut showed no compound looping, the greatest complexity being the development of an inflection in the second section and of a single loop in the anterior part of the final section of the gut. At this size the gut resembles that of *B. aeneus* about 50 mm long.

In a study of a collection of 37 fish of less than 100 mm, three individuals between 55 and 78 mm long were found in which the gut had the simple 'N' form characteristic of *B. aeneus* less than 25 mm long, the second section being straight and lacking the inflection which is evident in *B. aeneus* of 35 mm (Figure 5). These individuals appeared to be somewhat more slender and to have more acute heads than other material of *B. aeneus* of a similar size and the 78-mm individual had eaten several cyprinid fry, an item found in the gut of only one of the 682 *B. aeneus* examined, an individual 202 mm long.

Although no further material was available for study, it appears that the morphology of the gut may prove to be a useful criterion for distinguishing between juveniles of the two species at sizes which cannot readily be separated on quantifiable external characters.

## Discussion

There was considerable individual variation at any given size in the proportions of the various gut sections. In Figure 2, specimen K, although longer than L, had less well-developed coiling of the gut. This may simply represent individual variation. On the other hand, if gut morphology is dependent on age rather than on size, it could reflect the presence, amongst a cohort, of rapidly growing 'shoot fish' such as develop among carp in the presence of intense competition for food (Wohlfarth 1977). A further alternative is the possibility that occasional hybridization may occur between *B. aeneus* and *B. kimberleyensis*.

Change in the ratio of gut length to fish length during

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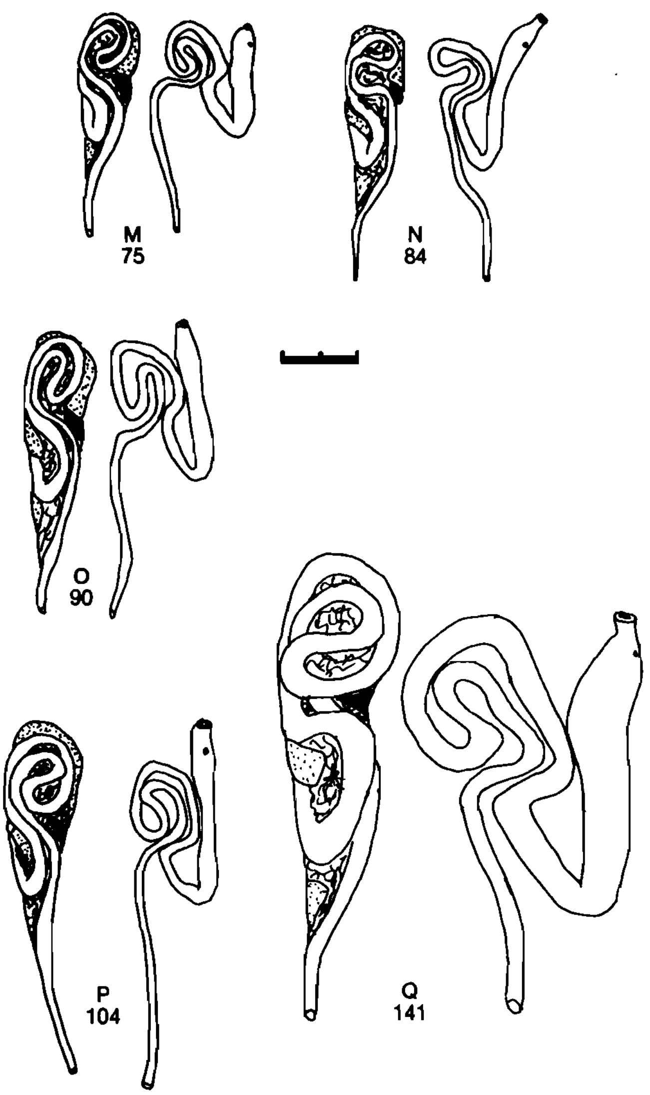

**Figure 3** Camera lucida drawings of alimentary viscera of immature *B. aeneus* 75 to 144 mm in fork length. Shading and conventions as in Figure 2.

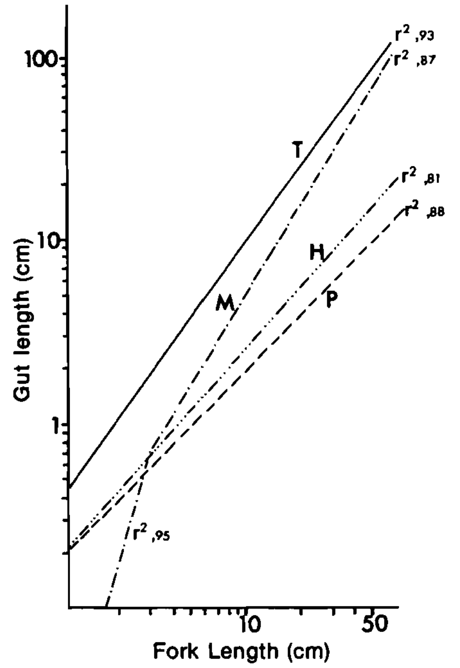

**Figure 4** The relationship between gut length and fork length in *B. aeneus*. T: total gut length; P: length of pseudogaster; M: length of mid-gut; H: length of hind gut.

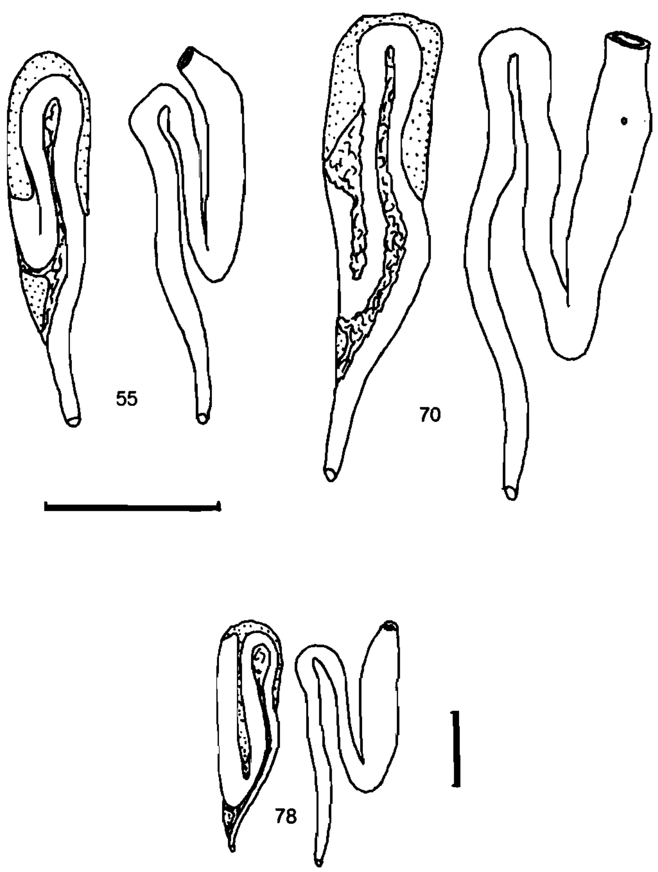

**Figure 5** Camera lucida drawings of the visceral mass and dissected alimentary canal of *Barbus kimberleyensis* from 55 to 78 mm in fork length. Conventions as in Figure 2. Scale bars 10 mm.

growth may, in part, be associated with the need to increase the surface area of the gut at a rate closer to the rate of increase in the mass of the fish than would be the case if gut development were isometric. On the other hand it may also allow a longer passage time, and thus a greater opportunity for digestion, for the lower energy food items which are taken by the larger fish.

Animal prey items offer a high-energy food resource but, with the exception of fishes, crabs, molluscs, amphibia and some of the larger insects, the bulk of those available in the aquatic environment are small forms such as chironomid larvae, copepod, ostracod and cladoceran crustacea and oligochaetes. Above a certain size of fish the 'profit', in energetic terms, of exploiting relatively scarce but energy-rich animal food is dissipated by the 'costs' of searching and ingestion. At this size the utilization of more abundant, or larger, but less energy-rich vegetable food resources may become energetically attractive. The size at which this occurs will be related to the degree of morphological and behavioural adaptation of the fish to animal food, and such a change is not found in specialized predators and planktivores.

*B. aeneus* has a relatively small mouth and cannot take large prey, and also lacks the heavy pharyngeal dentition needed to crush large molluscs or crabs. It is therefore constrained to alter its diet to one with a greater proportion of vegetable matter, although it continues to eat any animal material which becomes available. The relative increase in gut length with increasing fork length, and the appearance of a second loop in the gut at the length where animal food becomes less important, allows large *B. aeneus* to utilize vegetable matter more effectively. This utilization is, however, not efficient, at least in the context of the recently impounded P.K. le Roux

Dam where the main vegetable foods available are filamentous algae and angiosperms (Eccles 1984), although it may have been more efficient in its original riverine habitat where benthic diatoms are important and where considerable quantities of lamellibranchs are eaten (Skelton & Cambray 1981).

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