THE PANTANODONTINAE, EDENTULOUS TOOTHCARPS FROM EAST AFRICA

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INTRODUCTION

THE Pantanodontinae, a new subfamily within the oviparous Cyprinodontidae or "killifishes", was erected by Myers (1955) to accommodate a single genus and species, *Pantanodon podoxys* Myers, based on two small specimens from Dar es Salaam in Tanganyika which entirely lacked jaw teeth. They were briefly described as " Somewhat similar to *Procatopus* but with no teeth in the jaws and ventral rays spiny." No fuller description has since been published.

Recently five more edentulous toothcarps were found in a salt evaporating pool near Gongoni on the Kenya coast, some twenty miles north of Malindi. All are apparently females, mature at less than 20 mm. standard length, and all have normal pelvic fins. They have been compared with a paratype of *P. podoxys*. I must express my gratitude to Prof. G. S. Myers, of Stanford University, California, for lending me this specimen.

The Tanganyika specimen is a male of 30·5 mm. standard length. I can find no difference in meristic characters between this fish and the Kenya specimens, and such proportional differences as exist can be accounted for by its larger size and by sexual dimorphism. However, some male toothcarps are smaller, often considerably smaller, than females of the same species, and although this dimorphism is more marked amongst viviparous than oviparous forms, it is nonetheless surprising to find a male of apparently the same species so much larger. But I do not think this justifies placing the Kenya specimens in a separate species, at least until some Kenya males can be found. The Kenya population was confined to a highly saline pool, whereas the Tanganyika fishes are labelled as found in " swampy land a few miles inland." Thus the Kenya fishes may belong to a runted population living under adverse conditions. Runting is not rare amongst toothcarps.

The Sub-family Pantanodontinae : Relationships

The need for a full revision of the oviparous toothcarps, and especially the African Cyprinodontidae, has become obvious in attempting to establish the relationship of *Pantanodon* to other forms. Some characters used in the following comparisons cut right across the present subfamilial (or tribal) boundaries and yet appear to be equally as " stable " or " important " as characters now used to separate the subfamilies. The two or perhaps three distinct types of maxilla form, the presence of a forked or simple post-temporal, and the fusion of the median hypurals are examples which would seem to merit attention. Since a full revision has not been possible, I have used an existing classification following Myers (1955), and based mainly on earlier work by that author.

Family Cyprinodontidae—oviparous toothcarps

Subfamilies 1. Cyprinodontinae
2. Orestiatinae
3. Fundulinae
4. Rivulinae
5. Procatopodinae (Aplocheilichthyini of Myers, 1931)
6. Pantanodontinae
7. Oryziatinae (Aplocheilini of Myers, 1931)
8. Lamprichthyinae (omitted in Myers, 1955)

(Subfamilies 3–8 were tribes in the subfamily Fundulinae of Myers 1931).

In male *P. podoxys* the anal fin is not modified into an intromittent organ and the genus must be presumed oviparous. This, and the closer affinity shown by *Pantanodon* to African rather than American or Asian genera, seems to reduce the chances that *Pantanodon* is an introduced species.

In attempting to establish the relationship of *Pantanodon* to other oviparous toothcarps, tooth form—a useful key character in separating both genera and subfamilies—obviously cannot be used. Myers (1938) felt that less reliance should be placed on teeth than had been given by Ahl (1924), but nonetheless he was obliged to follow Ahl in separating the genera *Platypanchax*, *Cynopanchax* and *Plataplochilus* solely on the

basis of oral dentition. Again, Myers (1931) found little to distinguish his subfamilies Cyprinodontinae and Fundulinae except tooth form (tricuspid teeth in the former).

The absence of jaw teeth in *Pantanodon* is of course remarkable ; indeed it is unique in the whole order Microcyprini. But evidence is given below supporting the hypothesis that degeneration of teeth is but one aspect of a series of modifications arising from specialisation to a purely filter-feeding habit. Such specialisation is suggested by the barely protractile premaxillaries, the modification of the gillrakers into fan structures, the form of the pharyngeal toothpads, and the tightly coiled gut. In all these characters *Pantanodon* departs, often markedly, from the normal cyprinodont pattern. The fact that specialisation has apparently been great enough to eliminate such a stable character as jaw teeth makes it necessary to seek phylogenetic relationships on the basis of characters other than those involved in feeding. Thus the absence of vomerine teeth in an edentulous fish such as *Pantanodon* may not necessarily betoken greater affinities with the subfamilies Fundulinae or Procatopodinae than with the Rivulinae, while a non-protractile premaxilla may well represent an adaptation paralleled by that found in the Oryziatinae.

The two principal characters which can be used to place *Pantanodon* are the fairly high-set pectoral fins and the moderately wide preorbital, and these suggest affinities with the Procatopodinae. The pectorals are not so high as for example in *Aplocheilichthys pelagicus*, but can certainly be considered " high " in comparison with the rivulin *Pachypanchax*. The width of the preorbital region presents a problem since the lacrimal is in fact very much reduced and is narrower even than is found in many Rivulinae. However, the preorbital region as a whole is a little wider than in the Rivulinae. The other characters which would link *Pantanodon* with the Procatopodinae are the absence of vomerine teeth (already commented on) and the absence also of pseudobranchiae. I have been unable to find further characters sufficiently consistent and trenchant to distinguish the subfamilies Procatopodinae and Rivulinae. Thus the presence of a forked or simple post-temporal, and the number of branchiostegal rays, varies within these two groups, as does also the point at which the gill membranes unite, the degree to which the maxillary tip is bound to the lower jaw by skin, and the form of the hypural rays. In cephalic squamation, *Pantanodon* differs from both the Rivulinae and the Procatopodinae. In addition, I know of no other oviparous genus in which the male pelvic fins develop spiny hooks.

Of the procatopodin genera, *Pantanodon* most closely resembles *Hypsopanchax* in the compressed and deep body form. It bears a great resemblance to *A. stuhlmanni* Ahl (which should perhaps be referred to *Hypsopanchax*). However in *Hypsopanchax* the gill membranes are united much further forward. In addition, the predorsal region in *Pantanodon* is shorter (much shorter in the male) than in any genus of the Procatopodinae, the general appearance being much more like the cyprinid than the cyprinodont habitus. The pelvic fins are united by a membrane in *Pantanodon*, similar to the condition in *Procatopus*, but the fin bases are not so far advanced as in the latter genus. There is, however, a strong resemblance between these two genera in body form.

The occurrence of *Pantanodon*, at least in Kenya, near the coast in pools whose salinity often exceeds that of the adjacent sea, makes a link with the Oryziatinae of

the Indo-Malayan region and Japan at least a possibility. *Oryzias*, the only genus, has high-set pelvic fins, no vomerine teeth or pseudobranchiae, no parietals (see Ramaswami, 1946), and the premaxillae are non-protractile. In addition, some species are extremely small, females of *O. minutillus* maturing at only 17 mm. (Smith, 1945). But in *Oryzias* the abdomen is not trenchant and the predorsal region is relatively much longer so that dorsal, pelvic and anal fins appear to be set further back.

The fishes of eastern Kenya are part of a general eastern river fauna which is found to the east of the Rift Valleys from the Zambezi to Somaliland. While certain genera (e.g. the cyprinids *Barbus*, *Rasbora*, *Labeo* and *Garra*) occur also in India, the region as a whole does not show any closer affinities with the Indian freshwater fishes than do other regions (e.g. to the west of the Rift Valleys). No genera of Cyprinodontidae are shared with the Indian region, although *Pachypanchax* and *Nothobranchius* are also found in the Seychelles. *Pantanodon* shows little affinity with either of these two rivulins. The only procatopodins which may occur in this eastern river fauna are *Aplocheilichthys stuhlmanni*, but Ahl (1924) does not mention the locality in Tanganyika from which his specimens came, and *A. myoposae* and *A. carlislei* of Natal.

A marine route of entry to the East African coast also suggests affinities with the cyprinodont *Aphanius dispar* (Rüppell). This species occurs for example in reef pools in the Red Sea (Marshall, 1952) and its range extends from N.E. Africa to the Arabian sea coast (Fowler, 1956). But although the body profile is much closer to that of *Pantanodon* than is that of *Oryzias*, the pectoral fins are set much lower, and the preorbital is narrower, the lacrimal overlapping the maxilla.

Thus *Pantanodon* seems to be an isolated form which has become highly specialised in many of those characters of most value in separating the subfamilies of the Cyprinodontidae. The erection of a monotypic subfamily on the basis of trophic adaptation is here felt to be justified because in *Pantanodon* modification has far exceeded subfamilial limits (i.e. supralimital specialisation in the sense of Myers, 1960). At the same time *Pantanodon* shows other marked differences from the Procatopodinae which are unconnected with feeding habits (head squamation, pelvic girdle and rays, narrow lacrimal), but in no case do these serve to link it more closely with the Rivulinae or any other subfamily. *Pantanodon* therefore appears as a highly aberrant form most closely allied to the Procatopodinae but whose inclusion in that subfamily would either destroy the value of the present definition of the subfamily, or so burden it with unique exceptions that as a working description it would become very clumsy. Thus on practical as well as biological grounds it seems more reasonable to separate *Pantanodon* from the Procatopodinae.

Sub-family Pantanodontinae : Diagnosis

Pantanodontinae Myers, 1955, *Tropical Fish Mag.*, March : 7.

Small oviparous toothcarps of the family Cyprinodontidae characterized by the complete absence of jaw teeth, apparently as a result of specialisation to a filter-feeding habit. Similarly, premaxillaries barely if at all protractile, and gut tightly coiled. Gillrakers slender, but able to expand into minute triangular fans.

No vomerine teeth. Pharyngeal bones bearing transverse bars on which rows of fine teeth are set. Pectoral insertion moderately high. Dorsal short, set behind anal

origin. Distal part of the maxilla closely bound by skin. Epiplurals simple. Pre-orbital wide, about half eye diameter. Gill membranes united well behind posterior border of eye. In males ; the tips of the second, third and fourth pelvic rays are spiny and hooked.

Habitus. Body strongly compressed and abdominal region deep and trenchant, especially in males.

Genus *PANTANODON* Myers, 1955

Diagnosis as for species (see below).

Pantanodon podoxys Myers, 1955

(Text-figs. 1, 2 and 3)

Description based on five females from Kenya[1] (17–21 mm. standard length) and one paratype, a male, 30·5 mm. standard length from near Dar es Salaam, Tangan-
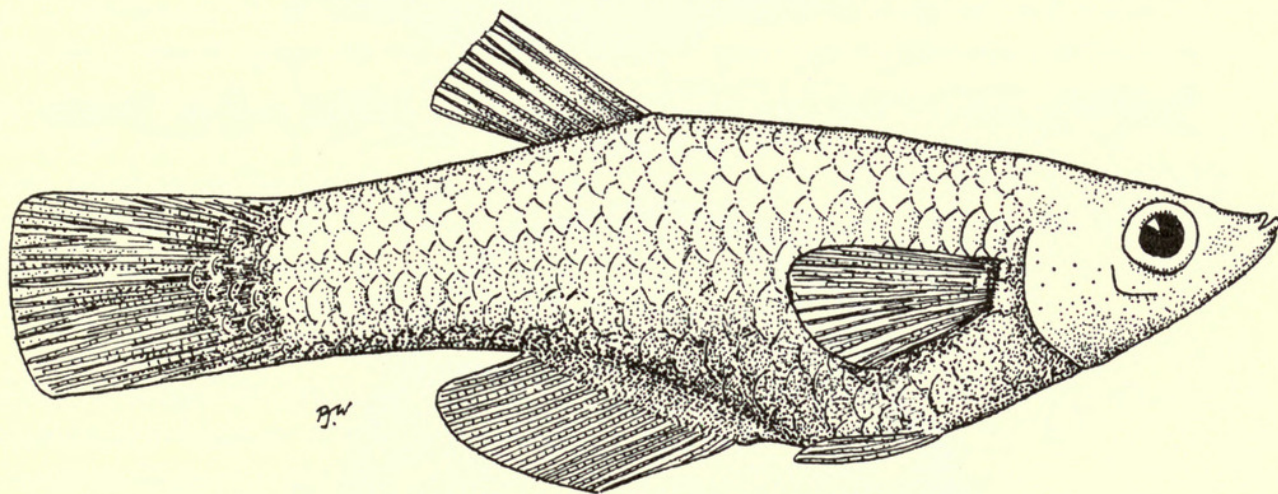

FIG. 1. *Pantanodon podoxys*, female, 21 mm. S.L.

yika. Skeletal elements are described from two of the Kenya specimens stained in alizarin. In the proportional measurements (in per cent. of standard length) and meristic counts, the first figure given refers to the male paratype, the figures in parenthesis referring to the Kenya specimens.

Depth of body 36·5 (27·5–29·5), head length 29·5 (31·5–31·8) ; eye diameter 8·9 (9·3–9·4), snout length 8·2 (8·6–9·4) ; predorsal distance 64 (65–69), pre-anal distance 57 (53–54) ; pectoral length, damaged (22·2 and damaged), pelvic length 13·5 (9·9–10·6) ; caudal peduncle, length 20·3 (22·5–23·4), depth 18·4 (17·3–17·5), length/depth ratio 1·11 (1·29–1·35).

Body deep, especially in males, strongly compressed, the abdomen trenchant. Snout, in profile acute, equal or just less than eye diameter. Upper lip broad and probably non-protrusible. No jaw teeth. Gill membranes free from isthmus, united behind posterior border of eye. Dorsal about equidistant from snout and tip of caudal rays, its origin over anterior third of anal fin. Pectoral fins set moderately

[1] B.M. (N.H.) No. 1962.4.4.1–2.

high, the first ray lying on the midpoint of body depth at that point, and just below horizontal through centre of eye ; pectoral base inclined forwards at 30° to the vertical. Pelvic fins short, normal in females but tips of 2nd–4th rays modified into
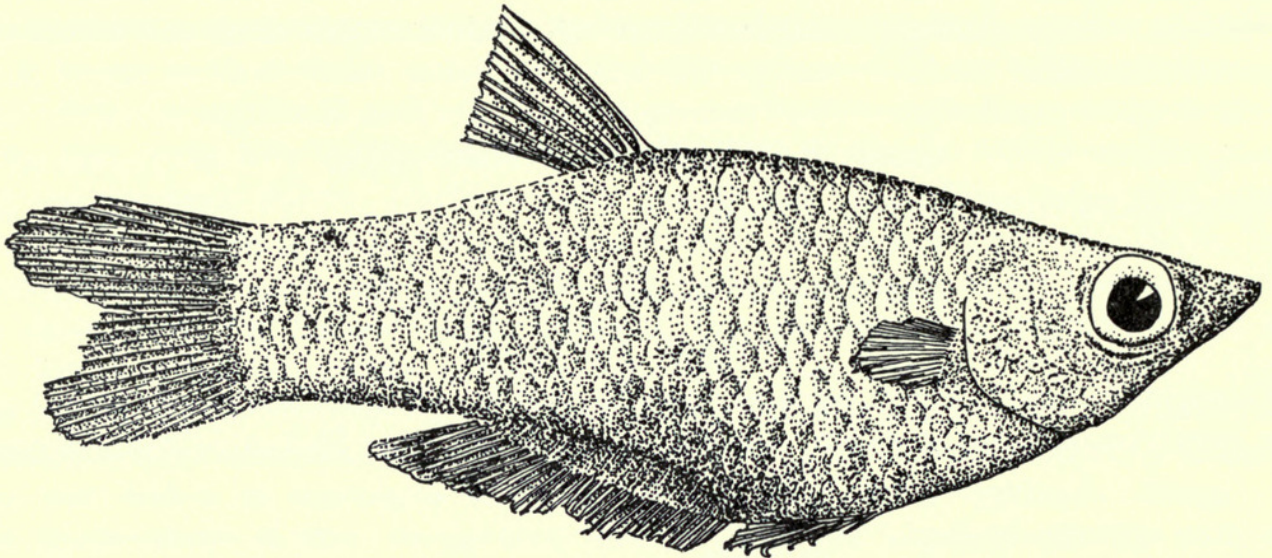

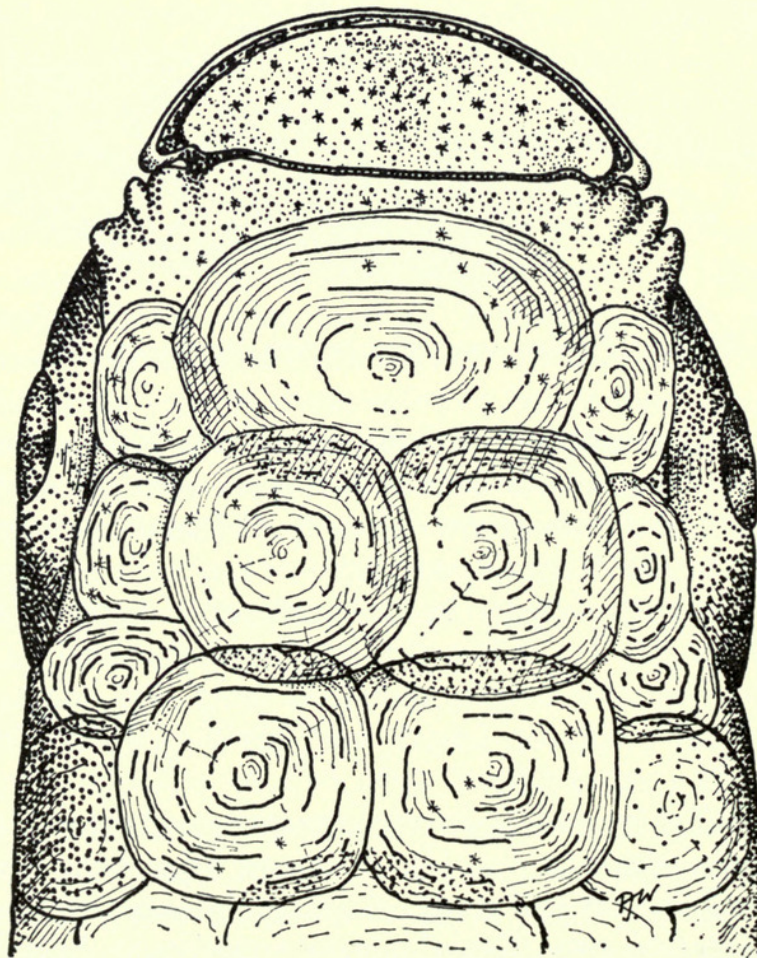FIG. 2. *Pantanodon podoxys* (male paratype, 30·5 mm. S.L.) Caudal, anal and pectoral fins damaged.

FIG. 3. *Pantanodon podoxys*. Dorsal view of head showing broad upper lip and arrangement of scales.

spiny hooks in males ; in both sexes just reaching anal origin. Caudal peduncle deep.

Dorsal i 6–7 ; anal ii–iii 17–18 (total 20–21), probably not produced posteriorly in either sex ; pectoral i 11, rounded in one female but damaged in others ; pelvic i 5, the inner edges membranously joined to body ; caudal 16–18 branched rays, 10–12 unbranched raylets, the posterior margin of the caudal bluntly round in females (damaged in paratype). About 60 gillrakers on lower part of first arch.

Scales in midlateral series 26–27 ; 9 scales between pelvic and dorsal origins ; 12 round caudal peduncle. Scales sharply bent in ventral midline.

Colour. In life, not recorded ; in preserved specimens, a uniform light brown with no distinctive colour markings, but scattered melanophores on head and lip.

Fins hyaline.

Jaw Teeth

These are entirely absent in *Pantanodon*. In sections of the upper and lower jaws of a specimen of 20 mm. S.L. there is no indication even of incipient tooth buds. The very small adult size attained by *Pantanodon*, the rather poor ossification of some cranial elements, the poor development of the head canals of the lateral line system, and the absence of jaw teeth, might all be ascribed to a neotenous condition. But jaw teeth in some toothcarps at least, appear very early indeed in ontogeny. They are present at birth in *Gambusia affinis* (Berner, 1947), are apparently fully formed in *Oryzias curvinotus* of 23 mm. (Nichols & Pope, 1927) and can be seen quite clearly in *Lebistes reticulatus* of only 17 mm.

It is also arguable whether the jaw teeth of *Pantanodon* degenerated under some kind of selection pressure, or whether their incidental loss (through mutation) then stimulated further adaptation to filter-feeding. It is, however, difficult to imagine disadvantages so great that teeth would become a hindrance to be actively selected against. On the other hand, the degeneration of teeth in fishes primarily adapted to seizing and grasping prey would place at great selectional advantage any subsequent adaptations which would assist in filter-feeding.

Pantanodon could perhaps represent an end-point in the reduction of jaw teeth shown by *Hypsopanchax* from the *Aplocheilichthys* condition.

Upper Jaw (Text-figs. 4 and 5)

In *Pantanodon* the upper jaw is barely, if at all, protractile, thus resembling *Oryzias* alone among the Cyprinodontidae. It is, however, difficult to be certain of the degree of protractability of the jaw in such small specimens, especially after preservation in formalin.

Details of the upper jaw mechanism are shown in Text-figs. 4 and 5. The premaxillae are expanded in the midline but do not meet. The descending ramus of the premaxilla is moderately broad and loosely attached distally to the lower jaw so that depression of the latter tends to draw not only the lower ramus but the entire premaxilla forwards very slightly. As a result of this, the upper portions of the premaxilla are raised slightly so that the premaxillae appear to open rather as a flap

upwards rather than to be protruded outwards. The maxillae are very slender. The upper ramus lies beneath the expanded portion of the premaxilla and is curved inwards. The descending rami overlap the distal tip of the premaxillae but are curved forwards. Upper and lower rami of the maxilla meet at a weak joint whose shape suggests that it might accommodate the posterior edge of the premaxilla but,
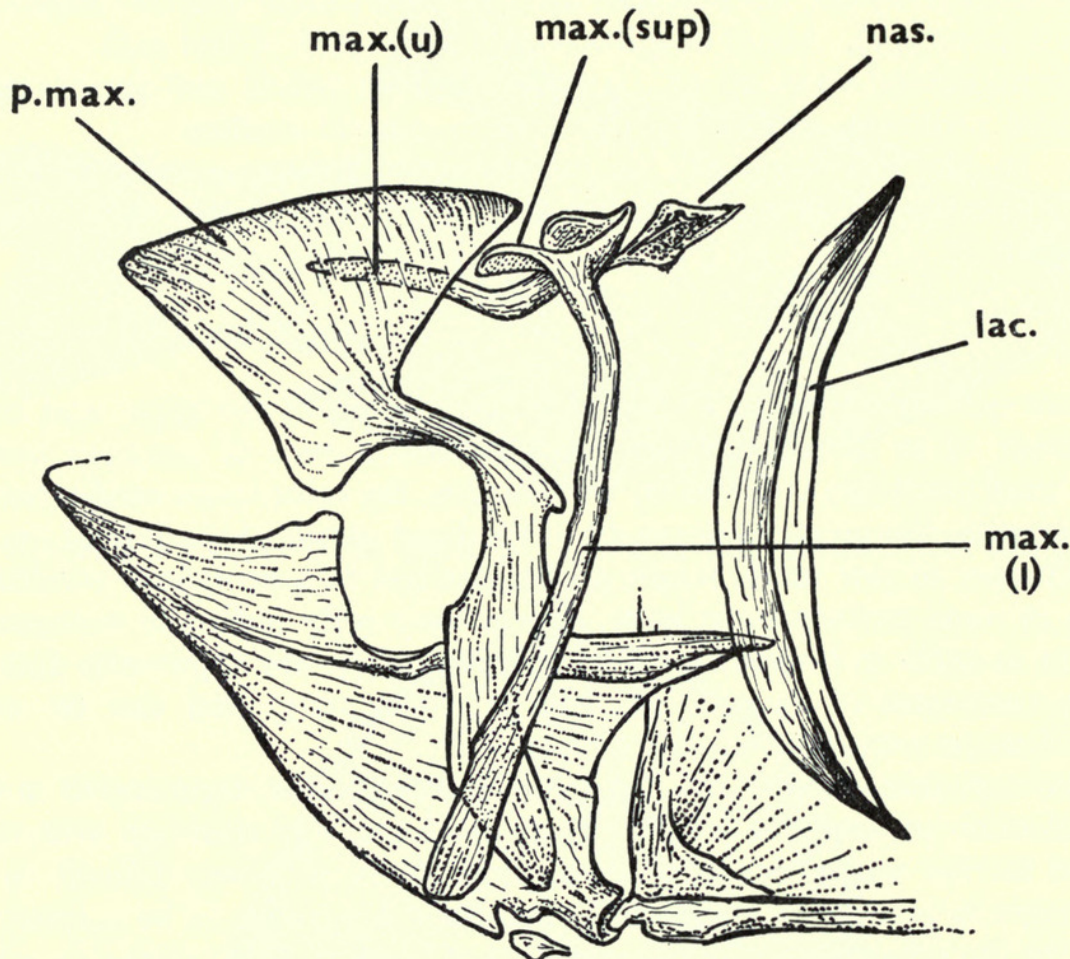
FIG. 4. *Pantanodon podoxys*. Left lateral view of jaw mechanism.

p. max. Premaxilla (upper ramus).
max (u). Upper ramus of maxilla (=inferior lobe—see text).
max (sup). Superior lobe of upper maxillary ramus.
nas. Nasal.
lac. Lacrimal or preorbital.
max (l). Lower ramus of maxilla.

owing to the distance between the two, in fact it does not. The lower ramus of the maxilla is produced slightly beyond its junction with the upper ramus and similarly the upper ramus projects beyond this junction also. The rami thus meet edgewise and so a forward movement of the distal tip of the lower ramus can through a twisting action, impart a forward movement also to the upper ramus. In the Microcyprini the mechanical principle involved in the protrusion of the premaxillae differs from that found in other groups (except perhaps the Mugiloidea). Eaton (1935) describes it as the Cyprinodont or twisting type, in which twisting of the lower end of a bow-shaped maxilla imparts a forward thrust to the upper maxillary ramus and

this in turn pushes out the premaxilla. This appears to be mechanically possible in *Pantanodon* but it is hard to say if it is in fact used.

Gosline (1961) has, however, challenged Eaton's view, believing the resemblance between say *Fundulus* and *Mugil* as far as jaw mechanism is concerned to be superficial and secondary. " The maxilla (i.e. in the toothcarps) apparently has very little to do with premaxillary protrusion " (Gosline *loc. cit.*), the distal ends of the premaxilla being membranously attached to the coronoid portion of the lower jaw. He concludes that the Microcyprini have a basically fixed premaxilla (i.e. no descending ramus in *Chologaster* and *Typhlichthys*) from which has later developed the protrusible upper jaw. Loss of protrusibility in *Oryzias* and presumably in *Pantanodon* also, both of which have descending rami, would thus be a reversion to the primitive
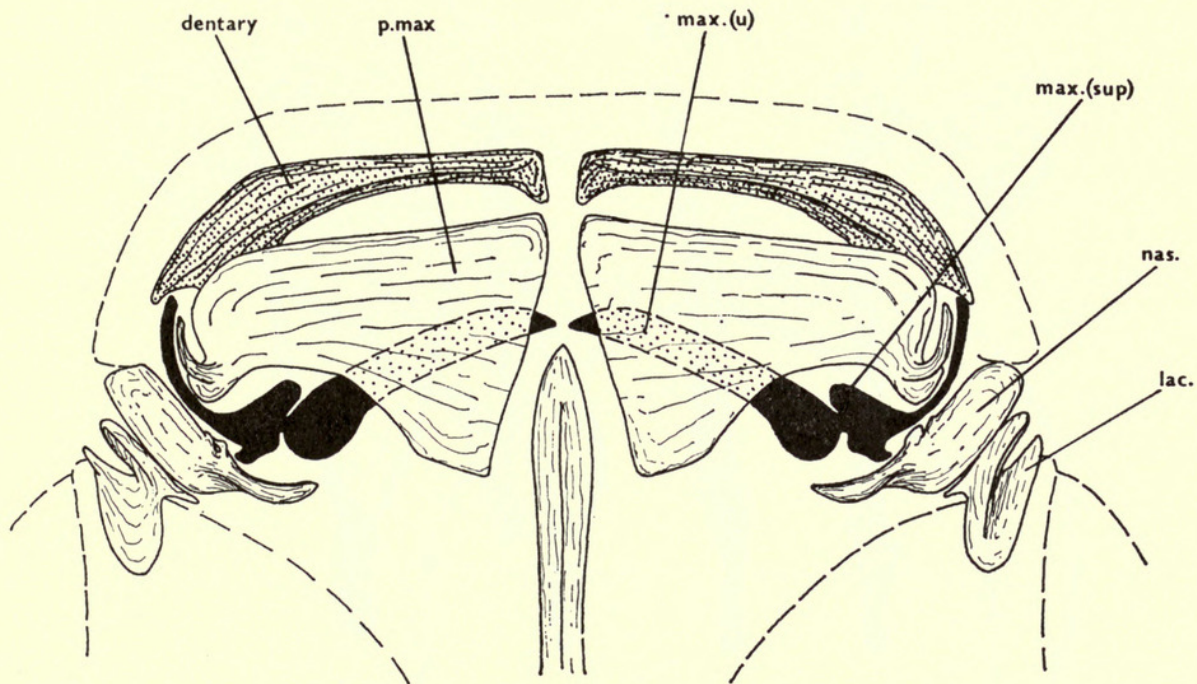

FIG. 5. *Pantanodon podoxys*. Detail of upper jaw structure, dorsal view, from an alizarin stained specimen of 17 mm. S.L. Symbols as in Text-fig. 4.

condition. But in *Pantanodon*, which shows so many structural changes apparently connected with feeding habits, one might expect a more slender lower premaxillary ramus than in fact occurs, although the maxilla in *Pantanodon* is by no means robust.

In *Pantanodon* the upper ramus of the premaxilla is fairly broad. A broad ramus is found in many other species, being perhaps best developed in *Aplocheilus lineatus* (see Ramaswami, 1946). Some species have a rather narrow ramus, e.g. *Micropanchax loati* and *Aplocheilichthys pumilus*.*

As already noted, at the point at which the upper and lower rami of the maxilla meet, there is a tendency for each ramus to be produced beyond the junction, especially in the case of the lower ramus. This latter projection, which may be more or less developed, is here termed the superior lobe, in contrast to the main upper maxillary

* The precise limits of *Aplocheilichthys* and *Micropanchax* still await definition. Here as elsewhere in the text, comparisons are essentially between species and not genera.

ramus, which is referred to as the inferior lobe (see Text-fig. 5). Of all the specimens examined, the inferior lobe lies underneath the expanded portion of the premaxilla, except where the premaxilla is too narrow for the two bones to meet. In all but two of the species examined, the superior lobe is no more than a small projection. The exceptions are *A. spilauchena* and *Procatopus nototaenia*, and in these two the superior lobe is greatly developed, reaching and overlying the expanded portion of the premaxilla. This seems to be an intermediate condition, for in those species with narrow upper premaxillary rami, there is only a single maxillary lobe, and from its position it appears to be the superior one ; however, in *M. loati* the superior lobe bears a small, pointed hook on its ventral surface and this may be a poorly developed inferior lobe. Thus there appears to be a gradual transition between forms with only a
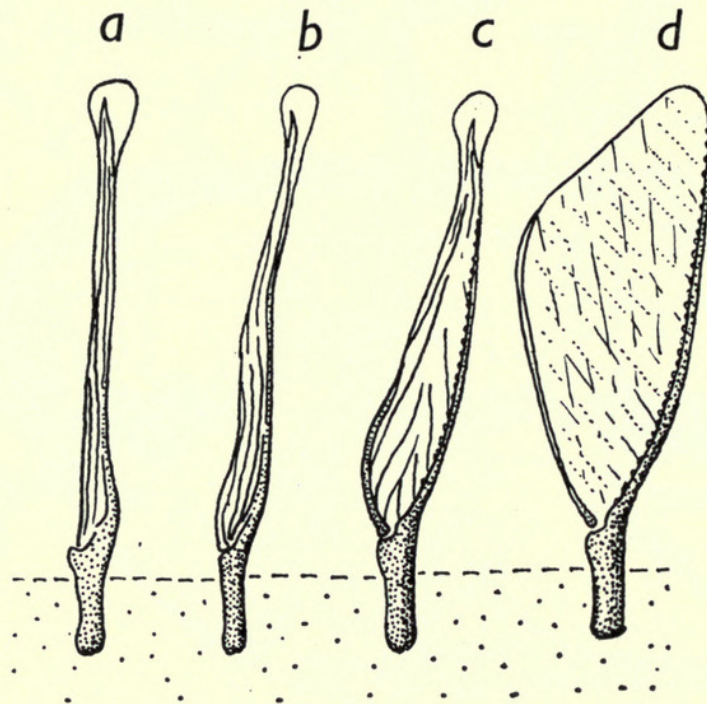

Fig. 6. *Pantanodon podoxys*. Gillrakers : probable stages in the expansion of the external series of gillraker fans. For explanation, see text.

superior lobe, through those with both lobes well developed, to those in which the superior lobe is small and insignificant. The number of species is, however, too few to show whether this is a line of development which can be related to the evolution of the major groups of oviparous toothcarps.

The Gillraker System (Text-figs. 6 and 7)

There are about 50–60 slender gillrakers on the anterior arch. In the specimens measured (15–20 mm. S.L.) the rakers are up to 0·8 mm. in length in the external series and about half this length in the inner series. In addition there is a single series of rakers on the antero-lateral edges of the lower pharyngeal bones ; these are essentially similar in shape to those of the external series on the other arches. Pharyngeal rakers have not been found in other Microcyprini examined (see below), but occur in some cichlids (e.g. *Tilapia*), in the cyprinid *Labeo forskalii*, and also in the Grey Mullet *Mugil cephalus*.

In situ the rakers appear as thin rods, about 100 μ thick and approximately this distance from each other. Each rod has a distinct globular cap and within the rod there is an inner core of bony tissue running the length of the raker and projecting slightly into the globular cap (Text-fig. 6*a*).

When, however, the gillrakers are removed from the arch, mounted on a slide in glycerine and subjected to slight pressure (on the coverslip), they show a more complex structure. The rods then expand into minute triangular fans, their apices being at the point of attachment to the gill arch. The internal and the external fans open in towards each other (i.e. towards the midline of the gill arch (see Text-fig. 7). Each
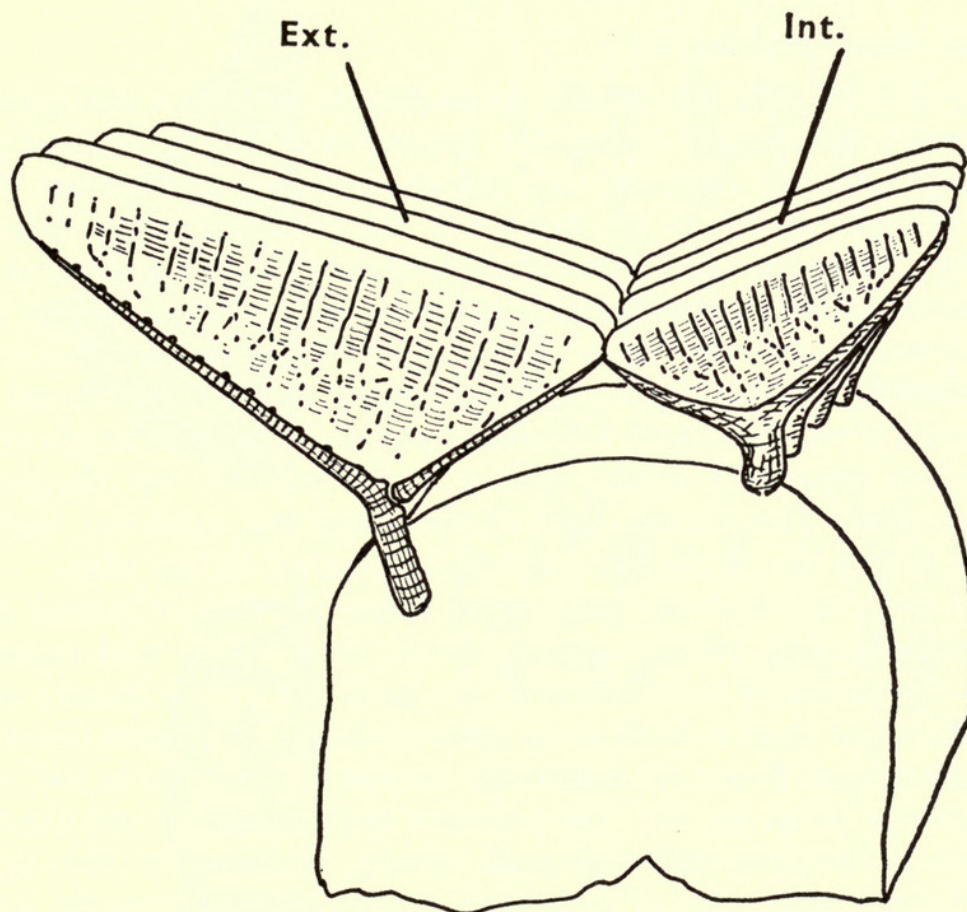

FIG. 7. *Pantanodon podoxys*. Gillrakers : cross section through gill arch showing reconstruction of probable shape and position of inner and outer gillraker fan series when fans are fully expanded. *ext.* external gillrakers. *int.* internal gillrakers.

fan has two thickened arms radiating from the apex. In the larger, external fans the subsidiary or smaller arm is distinctly jointed at its junction with the main arm, but this was not seen in the internal raker fans. At the apex of the fan is a small root. The distal edge of the fan is membranous and appears to be derived from the globular cap since the latter disappears in fully expanded fans. Text-fig. 6 shows a series of external raker fans in the process of expanding. In fully expanded fans there are about twenty fine parallel lines running at right angles to the membranous edge but not actually meeting it. Near the apex of the fan these lines tend to converge and form a reticulated pattern. Under very high magnification the lines resemble fine capillaries. If

this is correct, then their distension might well serve to erect the fan. At the same time their alignment also suggests that they offer support for the membrane of the fan. Between these " capillaries " the membrane is marked by a series of transverse lines, extremely fine and close together, which may be lamellae or ridges or even the structural supports of a very fine sieve. Such a sieve would be capable of retaining particles of about 2–3 μ in diameter.

The gillrakers and also the fans when erected, are probably capable of close inter-digitation. A discussion of the probable feeding mechanism in *Pantanodon* is given later.

The Pharyngeal bones (Text-fig. 8)

The pharyngeal toothpads also exhibit specialisation towards a microphagous diet.

The lower bones are roughly triangular, pointed anteriorly, rounded posteriorly (see Text-fig. 8a). Laterally there are three spines for muscle attachment, the anterior two pointing at right angles to the bone and the posterior spine directed rather postero-laterally. Along the antero-lateral edges of the bones lies a series of gillrakers. The two bones are neither suturally united nor even very closely apposed, resembling the condition found in some cyprinids. The ventral surface of the bones is composed of anterior radiating and posterior reticulated bony ridges. The dorsal surface is made up of a series of ten to thirteen transverse bars each bearing a single row of teeth. Anteriorly the bars are rather weakly joined in the midline, but the posterior two or three bars are free. The lateral edges of the bones are, however, fairly strongly ossified and the lateral tips of the bars are firmly attached to this edge.

The anterior teeth of the lower pharyngeal bones are slender, about 400 μ long, conical and pointed, quite widely spaced (about 300 μ apart) and curved slightly backwards. In the posterior rows, however, the teeth are a little shorter and become so densely packed that there is little or no space between their bases (Text-fig. 8b).

The upper pharyngeal bones are essentially similar in structure to the lower bones but are oval in shape (Text-fig. 8c). The posterior teeth are about 300 μ in length and about 100 μ apart, tricuspid with expanded crowns, as shown in Text-fig. 8d. The cusps show a distinct suture line at their base. In the anterior rows the lateral cusps are progressively lost until the teeth are conical in the anterior two or three rows. Generally, the teeth of the upper pharyngeals are rather more widely spaced than in the lower pads.

The Feeding Mechanism in Pantanodon (Text-figs. 9, 10 and 11)

Divergence of the Pantanodontinae has been almost entirely concerned with trophic adaptation to a filter-feeding habit. Specialisation towards a microphagous diet has apparently involved both the loss and modification of certain structures. Thus jaw teeth have been entirely lost which may preclude the seizure of prey in the normal cyprinodont manner. Secondly, the mouth gape is directed upwards while the pre-maxillae are more or less fixed. This precludes bottom-feeding and implies that *Pantanodon* must obtain its food from the surface layers. The third specialisation is in the form of the gillrakers. In order to understand their mechanism and possible

evolution from the more normal cyprinodont type, comparison was made, first with other Microcyprini, and then with other fishes which use the gillrakers to retain fine particles of food.

Aplocheilichthys pelagicus Worth., the small pelagic cyprinodont from Lake Edward, feeds mainly on small planktonic crustaceans and some insect larvae
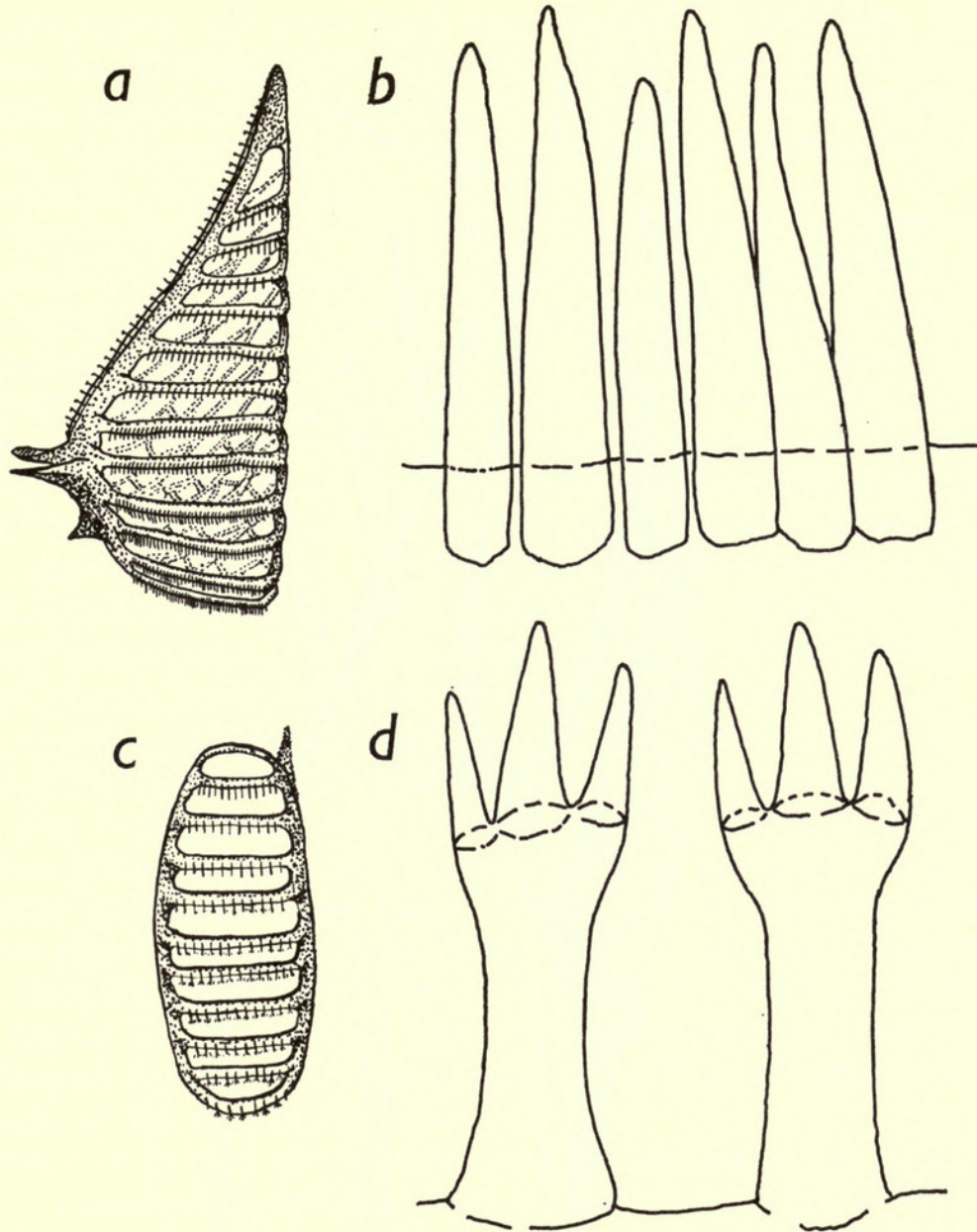

FIG. 8. *Pantanodon podoxys*. Pharyngeal bones and teeth from a specimen 17 mm. S.L.

    a. Lower left pharyngeal, dorsal view.
    b. Teeth from the posterior rows of the lower pharyngeal.
    c. Upper right pharyngeal, ventral view.
    d. Tricuspid teeth from posterior rows on upper pharyngeals.

(Worthington, 1932). In this species the internal gillrakers on the first arch are rod-like and do not expand, but the external rakers of the first arch are long, narrow plates set transversely to the line of the gill arch (Text-fig. 9). Alizarin staining suggests that, like *Pantanodon*, there is an inner and outer ossified support to the raker, but

that the lower and middle portions of the plates are also osseous. In the first four or five fans there is a curious tubercle projecting from the inner edge of the fan. The tubercle showed no apparent internal structure and its function is obscure. A narrow membrane runs the length of the inner edge of the fan, and the fans also have one or two fine lines running across their surface, encircling both the tip of the fan and the
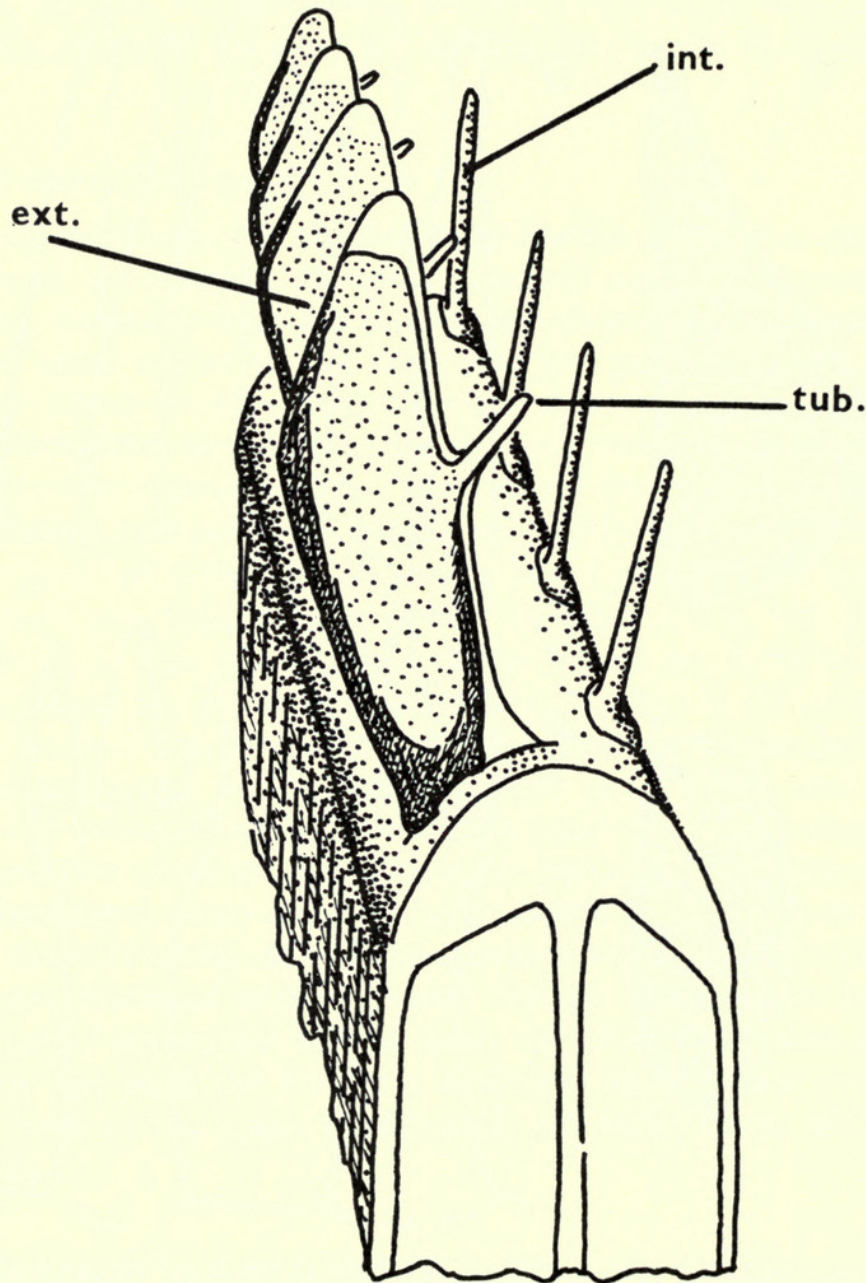

FIG. 9. *Aplocheilichthys pelagicus*. First four gillrakers on 1st gill arch, showing rod-like inner rakers (*int*) and plate-like external rakers (*ext*) which bear a small tubercle (*tub*).

base of the tubercle, joining in places and leading to the base of the fan. The structure of these lines is not clear ; in places they resemble spirally strengthened capillaries, while elsewhere they could be interpreted as mucus directing or deflecting ridges. In the succeeding arches the external rakers become pointed, and on the fourth arch they are toothed. The large and fairly widely-spaced pharyngeal teeth show that the

diet is composed of much larger particles than is that of *Pantanodon*, but the plate-like gillrakers on the first arch suggest that smaller particles may also be collected.

Plate-like gillrakers occur in a number of toothcarps, usually only on the first arch, occasionally on the second or on the third, but never in the specimens examined did they extend on to the fourth arch as in *Pantanodon*. *Aplocheilichthys spilauchena*, *A. pumilus*, *Micropanchax loati*, *Pachypanchax playfairii* and an undetermined species of *Mollienesia* all have some development of plate-like gillrakers. In *A. spilauchena* the gillraker plates are not set at right angles to the gill arch but are inclined slightly inwards and backwards, and at the same time the tips of the rakers lean forwards. Such an arrangement may be the case in *Pantanodon* but this could not be seen with the rakers *in situ*.

In many Cyprinodontidae the gillrakers are represented by teeth or tooth-like rakers on some or all the gill arches. The exact homology of these tooth-like rakers is not always clear ; some may merely be modified gillrakers, whereas others are probably teeth which have replaced the rakers. Here, all are referred to as " toothed rakers ". Toothed rakers are especially common on the fourth arch and parts of the third, but in some fishes are found also on the second and even the first arch. In most cases the toothed rakers are shield-shaped and lie flat against the surface of the gill arch and their distal edges bear numbers of fine teeth. Those of *Aplocheilus panchax* are shown in Text-fig. 10. Such toothed rakers occur in *Pachypanchax playfairii*, *A. spilauchena* and *Epiplatys sexfasciatus*. In *Aphanius dispar* the rakers of the external series on the first arch are tree-like and branched, while on the fourth arch they are identical in shape to the lower pharyngeal teeth.

In all the specimens examined, those with toothed gillrakers also had a series of minute microgillrakers on the external faces of all but the first arch. A single exception to this was *P. playfairii*. Microgillrakers were not found in any of the species with plate-like gillrakers. The microgillrakers are in many ways homologous with those of certain cichlid fishes (see Gosse, 1955 and Whitehead, 1959), but they are larger and are paired structures (Text-fig. 10). In *E. sexfasciatus* there are no micro-gillrakers as separate plates, but the base of each raker toothplate has at each corner a series of four or five fine-pointed teeth which evidently serve the same purpose. The disposition of the microgillrakers suggests that they are used to actively clean the raker teeth on the arch immediately in front.

Filter-feeding, or at least the collection and passing backwards of fine particles of food, presents a number of problems. Various methods have been evolved for solving these problems, one of which is the plate system of *Pantanodon*. Perhaps the greatest problem is the need to retain very fine particles by a device which will not clog. In the echiuroid worm *Urechis* this is solved by periodic swallowing of a very fine mucus sieve. In some fishes the cleaning of the sieve system appears to be achieved by the passage of a mucus film to which the particles adhere. The mucus stream must, however, be forced to take a direction different from that of the exhalent stream of water and it seems likely that plate-like gillrakers are at least partly responsible for creating the necessary turbulence for this to happen. In part, also, the shape of the branchial cavity will assist in forcing the mucus back towards the oesophagous, the principle being similar to that of a plankton net. In such a system

it would seem that mucus-coated plates would provide a greater collecting surface than would a plain sieve.

A plate system is used by species of *Labeo* (see Text-fig. 11), while the grey mullet *Mugil cephalus* employs a sieve. Comparing these two methods it would seem that the plate system can retain fine particles only in fishes as small as *Pantanodon* (i.e. about 20–30 mm. in length), whereas the sieve system is the more efficient in fishes of 100 mm. and more. *Labeo* is a highly specialized algal grazer, but in spite of inter-digitation of the gill plates, there is probably little need for the rakers to retain more
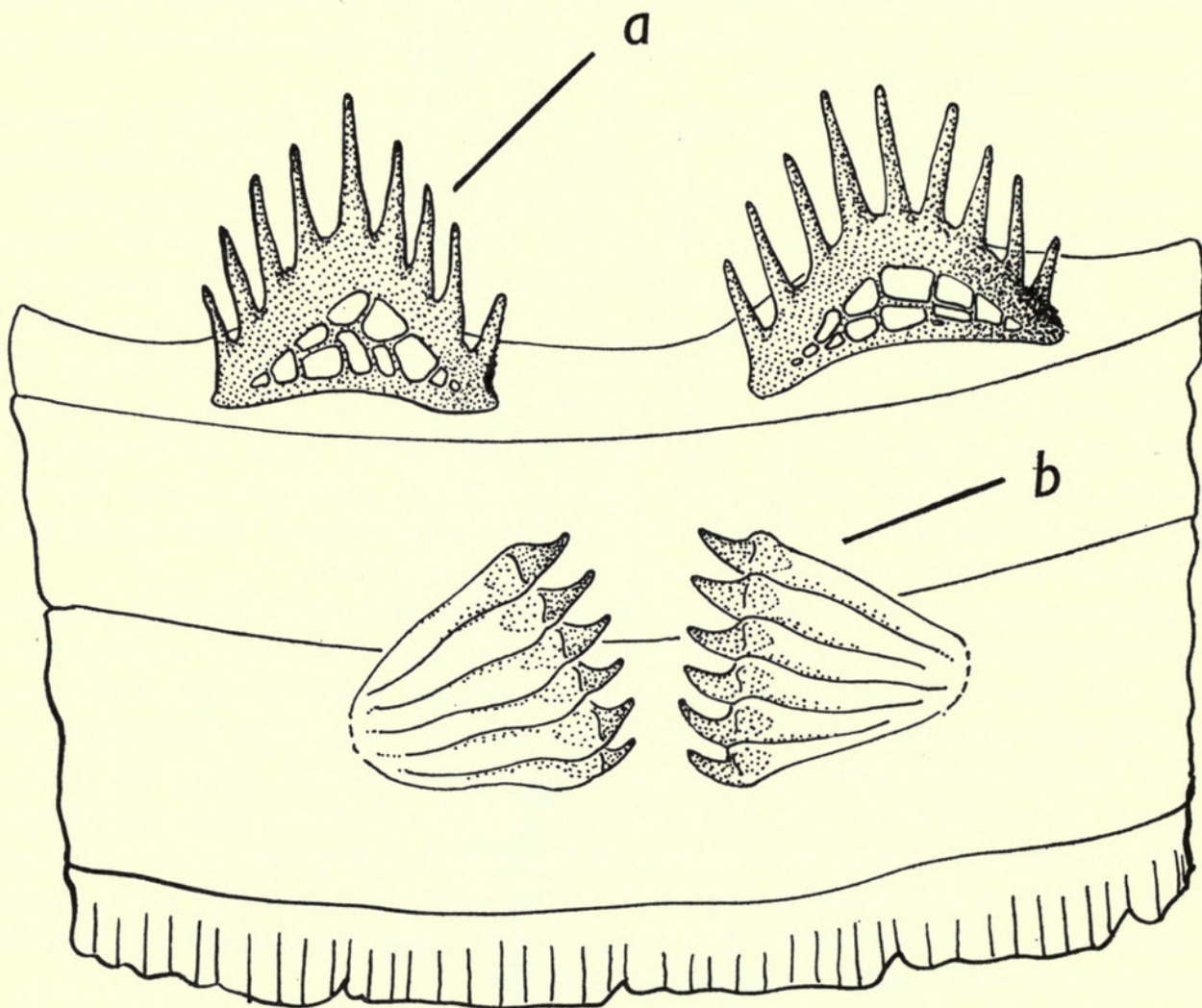

FIG. 10. *Aplocheilus panchax*. External face of second gill arch showing tooth-like gill-rakers (*a*) of external series, and position of micro-gillrakers (*b*).

than just the ingested algal fragments. In *Mugil cephalus* on the other hand the gill-rakers, which are long and very closely set, are joined at their tips and each gillraker bears a double series of minute projections along its length. The projections inter-digitate. In a 76 mm. fish, with gillrakers 2·0–2·5 mm. in length, the small projections were 50 μ apart. Each projection, however, bore a series of five to six minute spines along its upper edge, the tips of which were about 5–10 μ apart, and this presumably represents the size of the particles which can be retained. Like *Pantanodon*, *Mugil cephalus* has a series of pharyngeal gillrakers.

The form of the pharyngeal toothpads in *Pantanodon* differs so greatly from the normal pattern in other cyprinodonts (large, irregularly scattered teeth) that one must regard it as another manifestation of high specialisation to a microphagous diet. It is, however, difficult to imagine why a series of transverse rows of single teeth
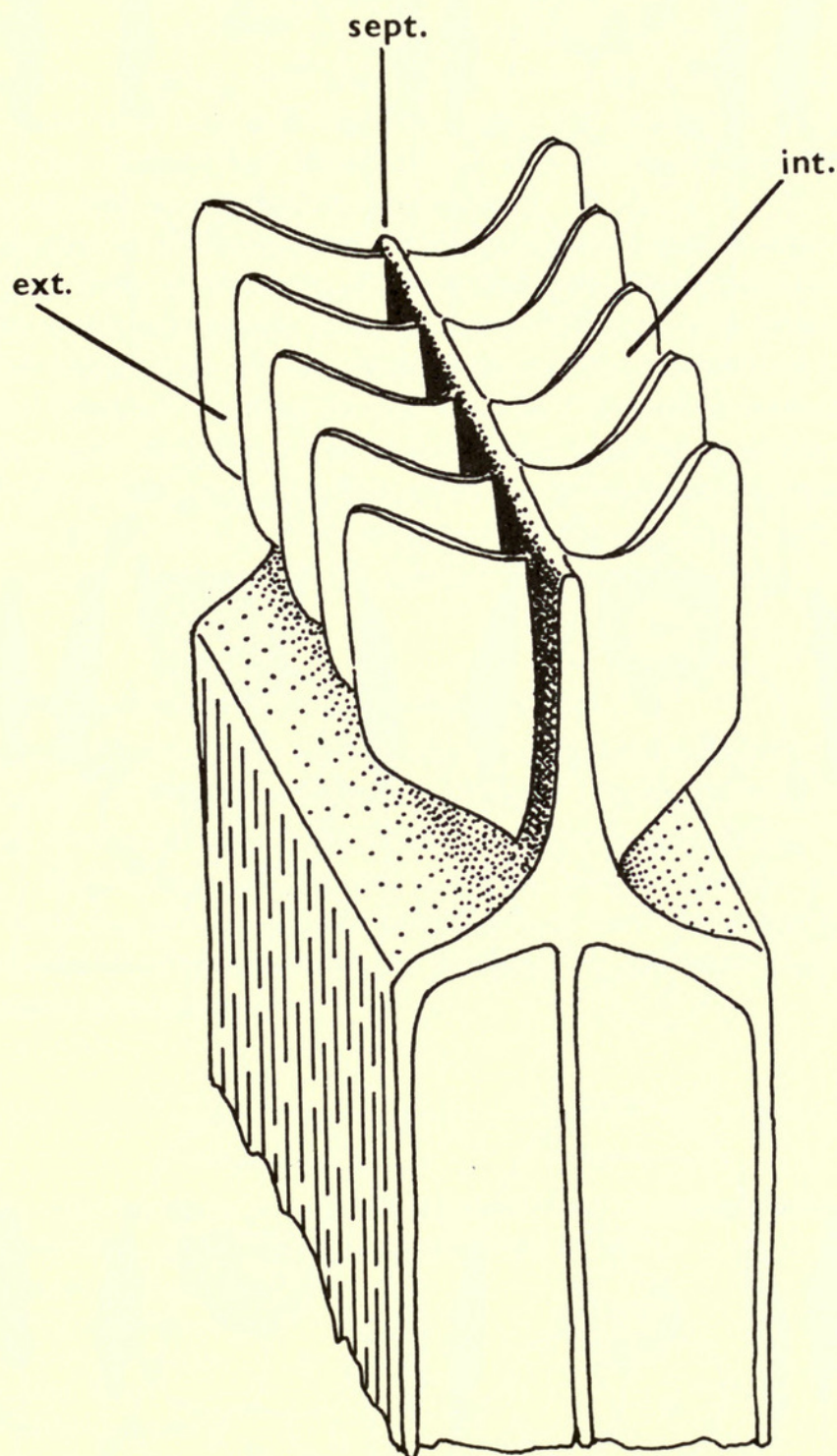

FIG. 11. *Labeo forskalii*. Plate-like gillrakers on the lower part of the 1st gill arch (semi-diagrammatic). Dorso-lateral view looking along gill arch from anterior end.

  int. Internal gillraker series.
  ext. External gillraker series.
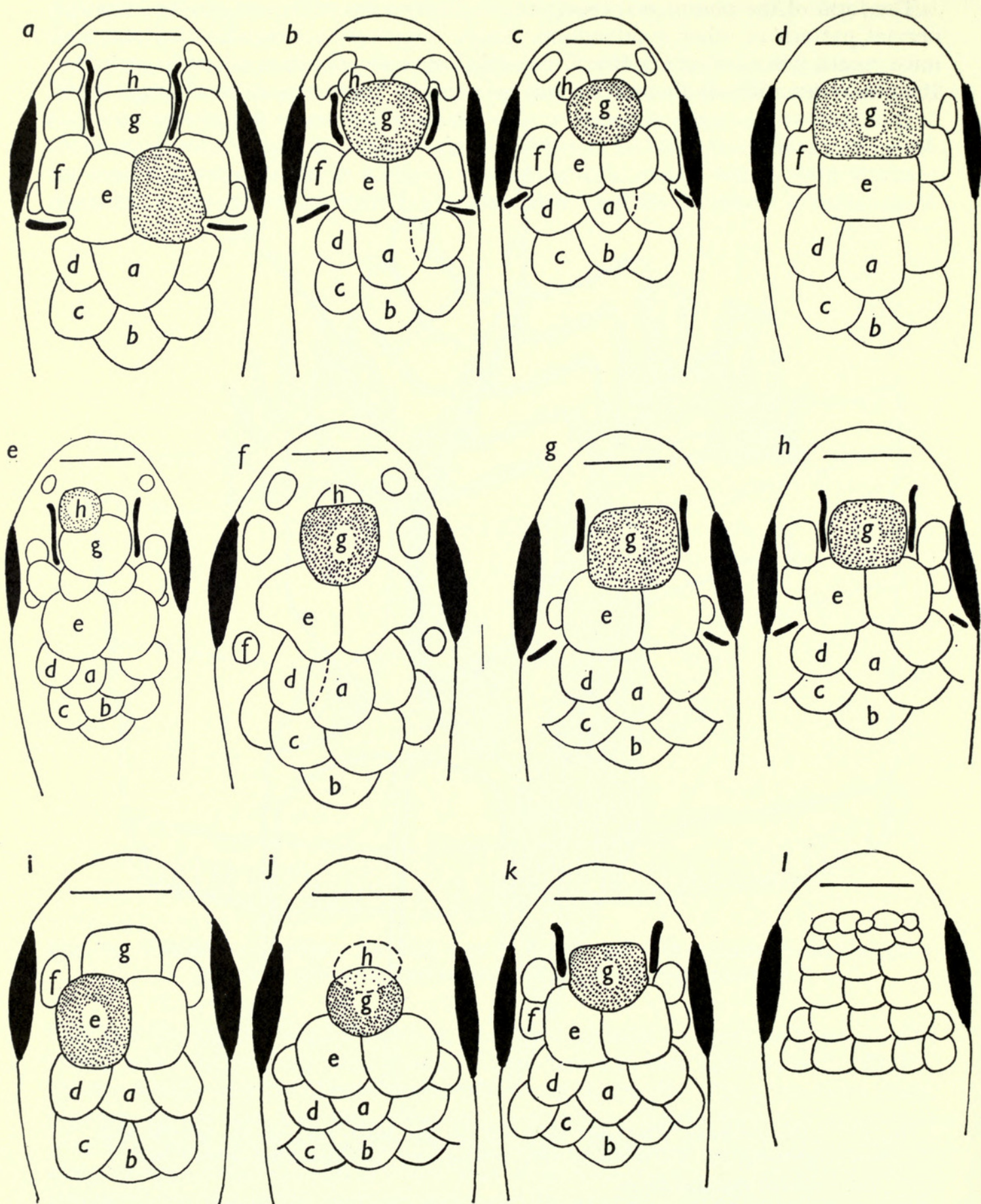 *sept*. Median septum between gillraker series.

FIG. 12.

should have arisen rather than a fine but dense mat of irregularly placed teeth, such as is found for example in the microphagous species of *Tilapia*.

In *Tilapia nigra*, which feeds principally on diatoms and is to some extent a filter-feeder, the lower pharyngeal bones are, as in other species, firmly united and cannot move laterally. In *Pantanodon*, however, the lower pharyngeals are only loosely connected, recalling the condition in *Labeo*, in which the bones are ventrally united by transverse muscles. Thus in *Labeo* and *Pantanodon* the lower bones may be able to move to some extent laterally, although in *Labeo* the bones are essentially used for grinding against the horny pad attached to the basi-occipital facet, whereas in *Pantanodon* they appear to act rather as combs.

The final adaptation in *Pantanodon* to a microphagous diet is seen in the very long and coiled gut. The form of winding of the intestine is highly characteristic. It first spirals inwards in a vertical plane, then reverses direction and unwinds in the same plane but on the other side of the peritoneal cavity. Suyehiro (1942) shows an essentially similar kind of winding in the case of *Chaetodon modestus* and *Siganus fuscescens*, but he notes that this form of intestinal winding is unusual. This type of coiling probably allows the maximum length of gut for a given volume of body cavity. The mucosa of the gut is formed into longitudinal zig-zag lines, but it is not known whether such a mucosal pattern can be related to a particular diet or if it holds any taxonomic value.

The Pattern of Cephalic Squamation (Text-figs. 12 and 13)

In a short but useful description of the patterns of scales found on the dorsal surface of the head in many Cyprinodontidae, Hoedeman (1958) showed that the African Rivulini bore less resemblance to the South American forms than they did to the Procatopodinae. Hoedeman considered only a single species of procatopodin, *Aplocheilichthys loati* (= *Micropanchax schoelleri*). I have examined also *Procatopus nototaenia*, *Aplocheilichthys spilauchena*, *A. pumilus*, *A. antinorii* and *A. pelagicus* and confirm Hoedeman's conclusion.

FIG. 12. Cephalic squamation in some Procatopodinae and Rivulinae (semi-diagrammatic). Topmost scale stippled. Scales lettered as explained in text.

    a. Aplocheilichthys spilauchena
    b. Aplocheilichthys pelagicus
    c. Aplocheilichthys pumilus
    d. Micropanchax loati
    e. Aplocheilichthys antinorii
    f. Procatopus nototaenia
    g. Aplocheilichthys cameronensis
    h. Epiplatys sexfasciatus
    i. Pachypanchax playfairii
    j. Nothobranchius guentheri (juvenile)
    k. Nothobranchius sjoestedti
    l. Nothobranchius taeniopygus (large adult).

In order to compare the rather characteristic pattern found in *Pantanodon* with those of other toothcarps, reference must first be made to the system of lettering individual scales employed by Hoedeman (*loc. cit.*). Although this system may occasionally imply a homology which in fact does not exist, nonetheless it is a useful method and one that is used here. The disposition of the head scales is to some extent governed by the position of the head canals. In most Rivulinae and Procatopodinae, there is a prominent pair of canals between the eyes, from the anterior rim of the orbit to about the middle of the orbit (absent, however, in *Pantanodon*); these represent the posterior portion of the supraorbital canal, or pores $2b$, 3 and $4a$ as designated by Gosline (1949). Immediately posterior to the eye is another part of this canal (pores $4b$, 5 and 6). From a comparison of my own material with the figures given by Hoedeman and also by Rosen & Mendelson (1960), the basic dorsal head scale pattern in the Cyprinodontidae appears to be reducible to three main elements.

A. Two lateral rows of scales between the anterior part of the supraorbital canal and the orbits themselves, but continuing forwards sometimes to cover the nasals. This lateral series is interrupted by the posterior part of the supraorbital canal. The most posterior scale of this series has been lettered f.

B. A median series of scales (single or paired) lying between the anterior parts of the supraorbital canals, reaching forwards to the lip in some cases, and backwards to a line joining the posterior orbital border. This series includes scales e, g, and h.

C. A circle of scales (b, c, and d) immediately posterior to the posterior part of the supraorbital canal. This circle of scales surrounds a single, median scale, a.

The pattern of squamation can also be characterized by the particular scale which overlies all the others; in Text-fig. 12, this scale has been stippled, and the fishes said to have a g, d or e-type pattern.

The Procatopodinae resemble the African Rivulinae in having a basic g-type pattern, with the e scale typically paired. However, in most Procatopodinae examined the a scale overlies the two d scales; occasionally one d may overlap the a, but rarely both. With one exception (*Nothobranchius guentheri*) the reverse is true in the African Rivulinae. Small differences such as this are remarkably stable within species and probably do hold a taxonomic weight. Modifications of this basic pattern occur in both subfamilies. In *Micropanchax loati* (Text-fig. 12d) the e scale is single and not paired as in all other African species examined. Hoedeman notes that *Pachypanchax* has an e-type pattern and I have confirmed that this is not merely a single, individual variant (Text-fig. 12i). An e-type pattern is also found in *Aplocheilichthys spilauchena*, but this appears to be the only other exception to the rule (Text-fig. 12a). In *A. antinorii*, possibly because of the small size of the specimens, the normal g-type pattern is upset (Text-fig. 12e), in the first place by an h scale overlying the g scale (this may be fortuitous, and does not seem to justify designation of an h-type pattern); and in the second place by two pairs of small scales immediately before and after the e scales. In Text-fig. 12 I have not labelled the anterior of these pairs since they appear to be too small to qualify as e scales. The posterior of these pairs I have considered to represent a paired a scale; this interpretation is not entirely satisfactory, but any other would involve an unlikely grouping of the d, c and b scales.

The most striking departure from the normal pattern is found in *Nothobranchius taeniopygus* (Text-fig. 12*l*). Here the scales are arranged in rows as on the body and do not conform to the circular pattern in other genera. A similar situation occurs in the larger specimens of the aberrant *Orestias*, the scales of the head being small and forming a mosaic pattern on the head. Hoedeman's figure for *O. agassiz* is probably derived from a small specimen; thus small specimens of *N. taeniopygus* have the
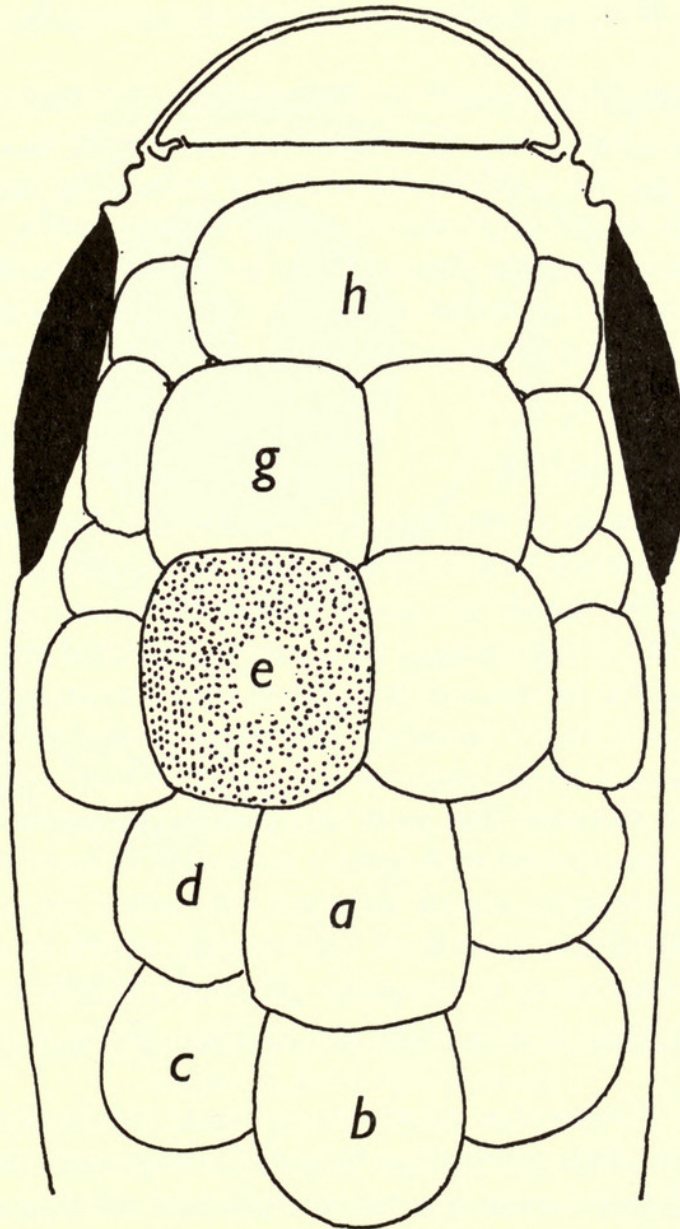

FIG. 13. *Pantanodon podoxys*. Cephalic squamation : topmost scale stippled. Lettering of scales as described in text.

normal circular pattern of scales but this is lost in the larger adults. The figure shown here for *N. sjoestedti* is based on a juvenile ; adults may well show the linear arrangement of scales found in *N. taeniopygus*.*

The scale pattern in *Pantanodon* is shown in Text-fig. 13. This differs from the usual

* However, Myers (1933) places *sjoestedti* in *Aphyosemion*, and the rather regular pattern of head scales would seem to confirm this.

pattern in that there are two rows of paired scales anterior to the *a* scale. Although this shows some similarity to the *A. antinorii* pattern, *Pantanodon* cannot be designated a *g*-type genus, and thus it differs from both the Rivulinae and the Procatopodinae. There are two or three possible interpretations ; the one shown in Text-fig. 13, which gives *Pantanodon* an *e*-type pattern, places the *e* scales after and not before the posterior margins of the orbits. To have placed them before would have required a very prominent position indeed for the *d* scales. The text-figure is based on two small specimens from Kenya ; unfortunately the somewhat larger paratype has few head scales.

Whatever interpretation is arrived at, *Pantanodon* evidently differs from both the Rivulinae and the Procatopodinae, although it seems closer to the latter, having the two *d* scales overlain by the *a* scale, and not the reverse (a further reason for considering the *d* scales to be correctly placed in the text-figure).

Clearly, the pattern of cephalic squamation could well prove a useful systematic tool for the Cyprinodontidae provided due regard is paid to the size of the individuals compared. At the same time, the true homology of the scales must be derived from ontogenetic studies.

Head Canal System (Text-fig. 14)

The degree of development of the sensory cephalic canal system has been shown to have systematic value in some toothcarps, at least where closed canals occur (Gosline, 1949). In *Pantanodon* the canals are much reduced and are open (see Text-fig. 14). The infraorbital canal (*C*) is represented by a short preorbital groove with three pores. The supra-orbital canal (*A*) is also much reduced, and is represented by a post-orbital groove containing pores 6 and 7 (possibly also 5) as designated by Gosline (*loc. cit.*). There is an indication of a single pore on the snout, which may represent pore 1 of the supraorbital canal. Between this pore and pore 6 the supra-orbital canal is either discontinued or firmly closed over with bone ; certainly there is no external indication of the usually quite prominent canals between the orbits found in almost all other Procatopodinae and Rivulinae examined, the portion which incorporates pores 2*b*, 3 and 4*a*. The preopercular canal is complete (*B*), and extends forwards to below the anterior border of the eye. Seven pores are visible. There is no mandibular canal developed.

The pore system in *Pantanodon* shows many basic similarities with other genera examined. The absence of the central portion of the supra-orbital canal may perhaps be rare amongst the African forms, but the mandibular canal is often absent (present in *Epiplatys sexfasciatus*).

The Skull

The small size of the specimens and in many places the rather weak ossification of the bones, have made it difficult to compare the shape, extent, or even the presence of some cranial elements. Thus I cannot be certain whether parietals are present or not although they appear not to be. Absence of a parietal would argue affinities with the Oryziatinae since, contrary to Regan (1911), parietals are absent in *Oryzias* (Ramaswami, 1946). But the sutures between the dermal roofing bones of the skull in

Pantanodon can rarely be seen. In general the skull shows no marked departure from the normal procatopodin type as regards shape and proportions, but some small differences can be noted.

The lacrimal (or pre-orbital) in *Pantanodon* is much reduced anteriorly, the bone consisting entirely of the trough-like groove for the pre-orbital canal. In members of the Procatopodinae the preorbital canal is but a small part of the lacrimal, the bone expanding anteriorly and to a greater or lesser extent covering the ventral portions of the descending rami of the maxilla and premaxilla. In *Pantanodon* there
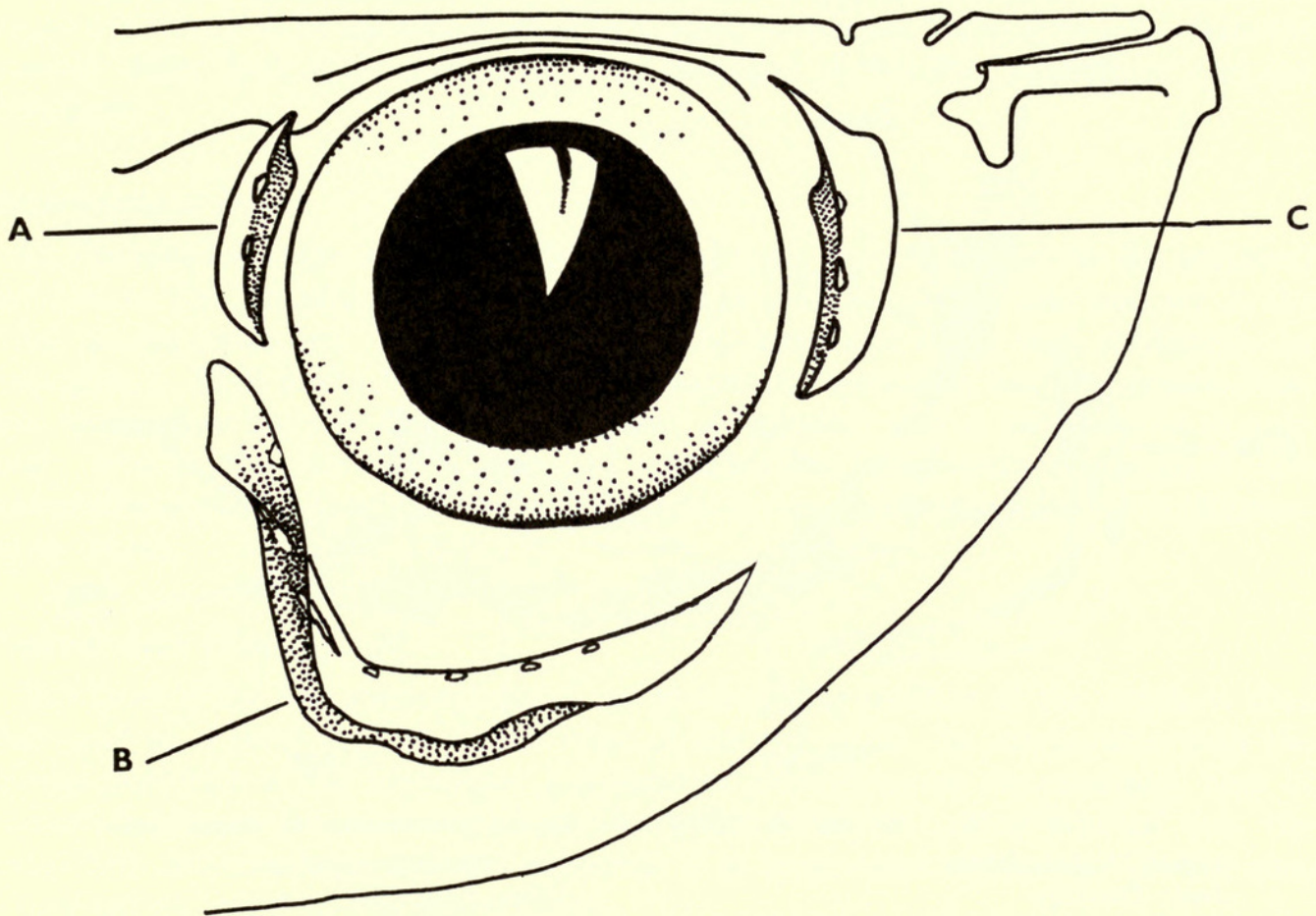

FIG. 14. *Pantanodon podoxys*. Cephalic canal system. A, supra-orbital canal. B, preopercular canal. C, infra-orbital canal.

is quite a wide space between the lacrimal and the maxilla and premaxilla tips. In the Rivulinae the lacrimal is to some extent expanded dorsally, but quickly tapers ventrally. On the other hand the whole preorbital region in this subfamily seems to be narrow, the anterior edge of the lacrimal again meeting and sometimes overlapping the maxilla and premaxilla. Myers (1931) uses the size of the preorbital in relation to the size of the eye (respectively more or less than half the diameter of the latter) to distinguish the Rivulinae from the Procatopodinae, and says that despite the rather larger eye in some fishes, this character is trenchant when use is made of comparative material. Although the lacrimal is strictly speaking very narrow in *Pantanodon*, I consider that nonetheless it represents a variation on the procatopodin pattern and is not referable to the rivulin type, principally because the preorbital

region *as a whole* (i.e. anterior orbital rim to corner of mouth) is as wide as in the former subfamily and not the latter.

The nasal in *Pantanodon* is also a rather narrow bone, in comparison with members of the Procatopodinae and Rivulinae, in which it often meets and overlaps parts of the maxilla and even the posterior part of the premaxilla.

The post-temporal is forked in *Pantanodon* (see Text-fig. 16), but this cannot be taken as a subfamilial character. Thus it is unforked in *Oryzias* (Ramaswami, 1946) ; forked in some Rivulinae (e.g. *Epiplatys sexfasciatus*) but not in others (*Aplocheilus panchax*, *A. lineatus* and *Pachypanchax playfairii*) ; unforked in some Procatopodinae
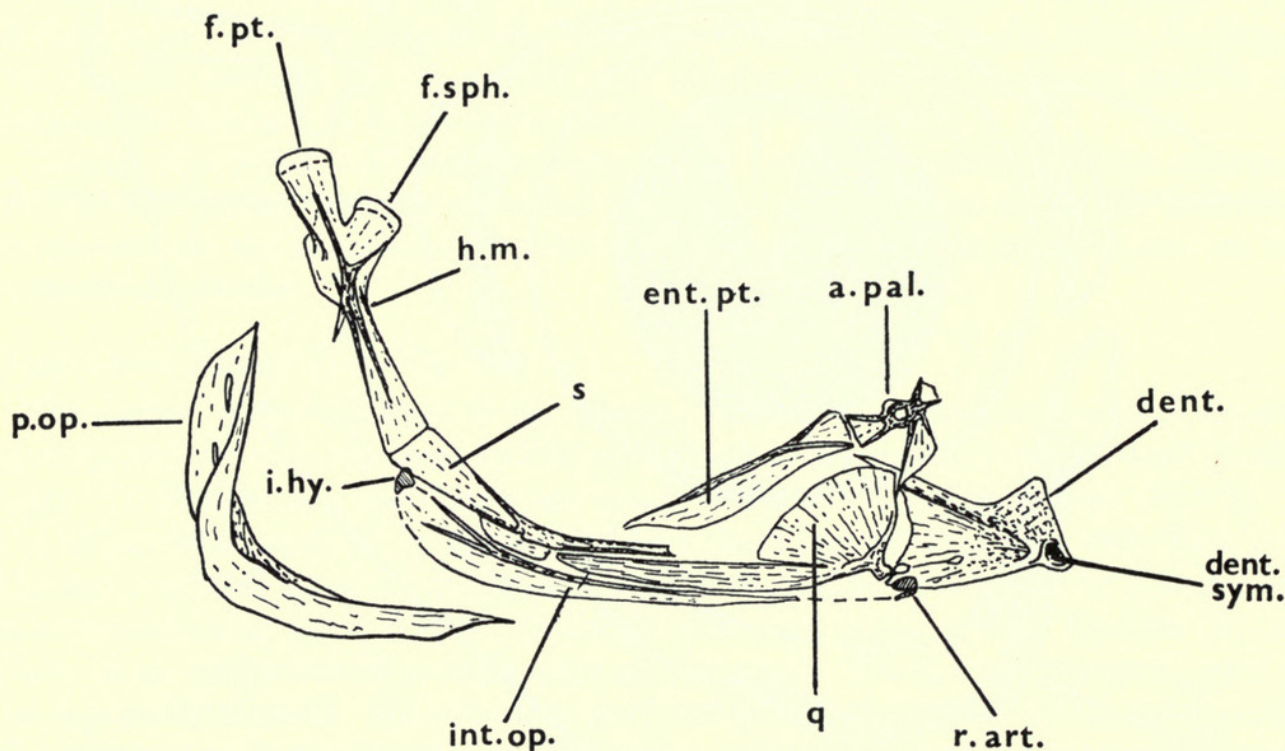

FIG. 15. *Pantanodon podoxys.* Hyomandibular and jaw suspension.

a. pal. Autopalatine	*h.m.* Hyomandibular
dent. Dentary	*i. hy.* Interhyal
dent. sym. Cup-shaped symphysis of the dentary	*int. op.* Interoperculum
	p. op. Preoperculum
ent. pt. Entopterygoid	*q.* Quadrate
f.pt. Pterotic facet	*r. art.* Retro-articular
f.sph. Sphenotic facet	*s.* Symplectic

(e.g. *Aplocheilichthys spilauchena*) but forked in others (*A. pelagicus* for example). The distal end of the main stem is flat and lies on the epiotic. The bifurcation of the post-temporal occurs more proximally in *Pantanodon* compared with other species in which this bone is forked.

The elements in the hyomandibular-jaw suspension series are generally rather weak and resemble those figured for *Oryzias melastigma* by Ramaswami (1946), but the articular facets of the hyomandibular are relatively large and there are two cartilaginous facets and not one (see Text-fig. 15). As in *Oryzias*, the symplectic is narrow and

there is no metapterygoid or ectopterygoid; Myers (1931) believed the former entirely absent from the whole suborder Poecilioidea, but Ramaswami (*loc. cit.*) finds a metapterygoid in *Aplocheilus lineatus*. The ventral arm of the quadrate is relatively long. There is a small retroarticular. The junction between the angular and the dentary is not well demarcated. The symphysial surface of the dentary is cup-shaped, and presumably accommodates a ball-joint of cartilage.

In the opercular series, the preoperculum is reduced (rather like the lacrimal) to a curved open groove containing the preopercular canal. The groove is not a surface formation, but is formed in the posterior and ventral edge of the bone, as Tchernavin (1946) has shown to be the case in all other Cyprinodontidae. Other opercular elements scarcely differ from their counterparts in members of the Procatopodinae and the Rivulinae.

Branchiostegal Rays

In *Pantanodon* there are five branchiostegal rays, three attached to the epiphyal and two to the ceratohyal. The number of rays varied between four and six in the other species examined. The number cannot be correlated either with subfamilies or even genera. Thus in the Procatopodinae, *Procatopus nototaenia* has six, *Aplocheilichthys spilauchena* has five, while *A. schoelleri*, *A. pumilus* and *A. pelagicus* have only four; and in the Rivulinae *Epiplatys sexfasciatus*, *Pachypanchax playfairii* and *Aplocheilus panchax* have six, while *A. lineatus* is reported to have only five (Ramaswami, 1946).

Pectoral Arch (Text-fig. 16)

The base of the first pectoral ray is set at about the midline of the depth at that place and on a level with the lower edge of the eye pupil. In comparison with the low-set pectorals of the Rivulinae (*Epiplatys* or *Pachypanchax* for example), that of *Pantanodon* must be considered high, although as Myers (1931) pointed out, the distinction between high and low pectorals is in some cases confusing. The fin base is inclined at about 30° to the vertical.

The pectoral arch is shown in Text-fig. 16. The bifurcation of the post-temporal occurs at the junction of this bone with the tip of the cleithrum, so that the expanded portion of the post-temporal is contained wholly on the cleithrum, and not merely its distal tip, as for example in *Epiplatys*. I have been unable to detect a post-cleithrum in *Pantanodon*; if present, this bone must be extremely small and weakly ossified, as in *Pachypanchax playfairii*. The pectoral radialia are weak and the fourth radial is barely apparent. The coracoid is not keeled ventrally, but has a narrow, more strongly ossified bar running diagonally to its anterior tip. The coracoid foramen is large. The scapula and the upper part of the coracoid are weakly ossified compared with the lower part of the coracoid (suggested by stippling in Text-fig. 16). There are twelve pectoral rays, the first three articulating directly with the edge of the scapula, the remainder with the radials.

The pectoral arch of *Pantanodon* shows no marked specialisation or departure from the general form found in the other genera examined. The distinction between

the high-set pectorals of the Procatopodinae and the low-set pectorals of the Rivulinae appears to be rather one of degree than of any structural difference. In the Rivulinae the cleithrum is less steeply inclined while, at least in *Pachypanchax playfairii*, the upper end of the cleithrum is not extended in compensation, but the post-temporal is much longer. As a result, the base of the first pectoral ray is brought on a level with the lower rim of the orbit. In the small Kenya specimens of *Pantanodon* the
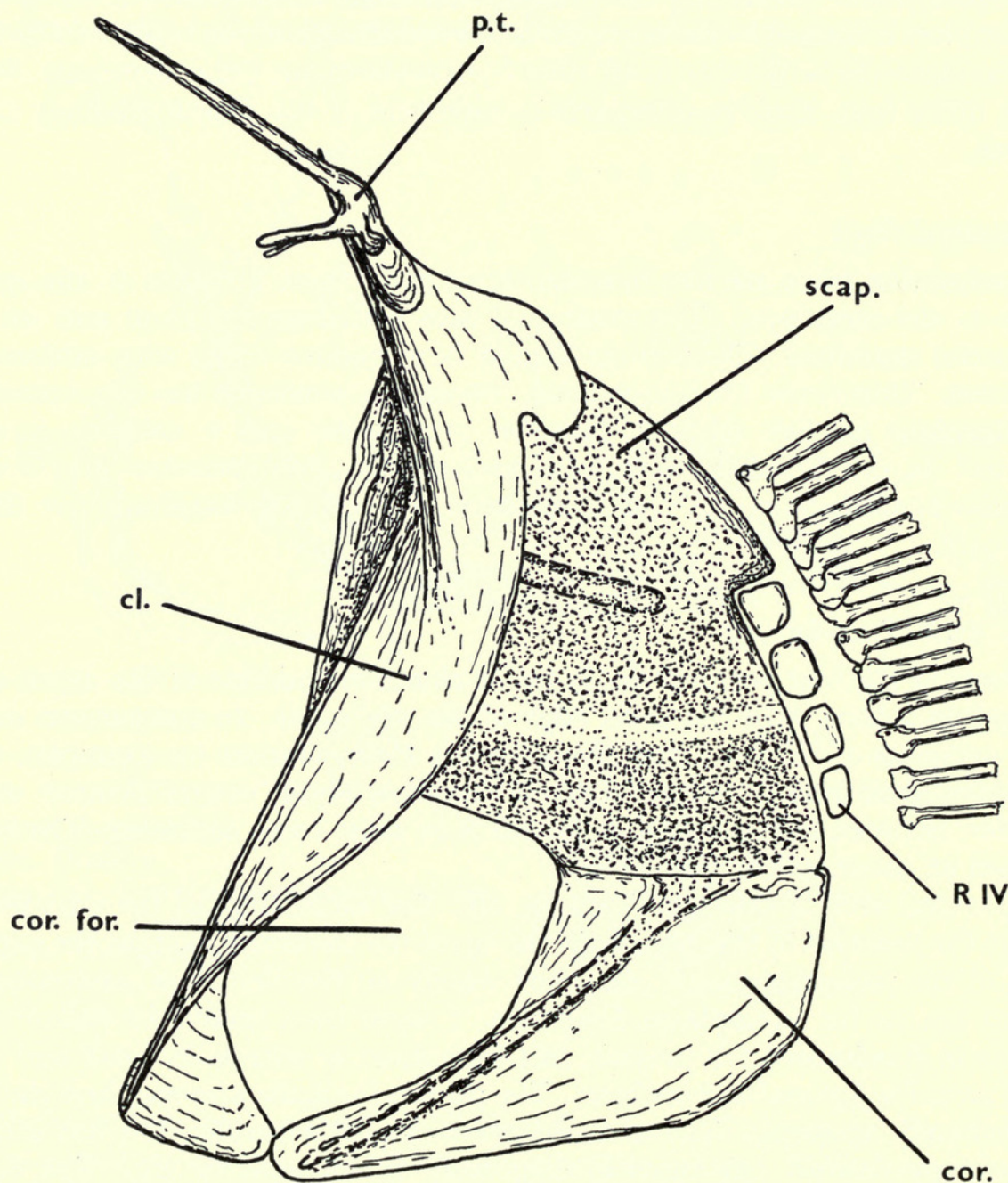
FIG. 16. *Pantanodon podoxys*. Pectoral arch (left, external face). From an alizarin stained specimen 17 mm. S.L.

p.t. Post-temporal   *cor. for.* Coracoid foramen
cl. Cleithrum   *scap.* Scapula
cor. Coracoid   R IV. Fourth radialia

first ray is level with the centre of the eye ; in the larger paratype, it is a little below this, but this may be due to the greater body depth of the paratype.

Pelvic Girdle (Text-figs. 17 and 18)

The pelvic support bones are T-shaped, with a very slender median portion (Text-fig. 18). In five other genera examined (*Procatopus, Pachypanchax, Aplocheilus, Micropanchax* and *Aplocheilichthys*) the median portion is very much broader than this. Judging from these five genera, there seems to be considerable variation in the shape of the two lateral processes of the pelvic support, the inner wings overlapping more or less firmly, and the outer wings in some cases being produced posteriorly, presumably for added support. There are no " splint " bones in *Pantanodon* such as described by Gosline (1961) for *Fundulus majalis* ; but this author notes their absence in another species of *Fundulus*, and the possession of splint bones may not hold much signficance in the Cyprinodontidae.
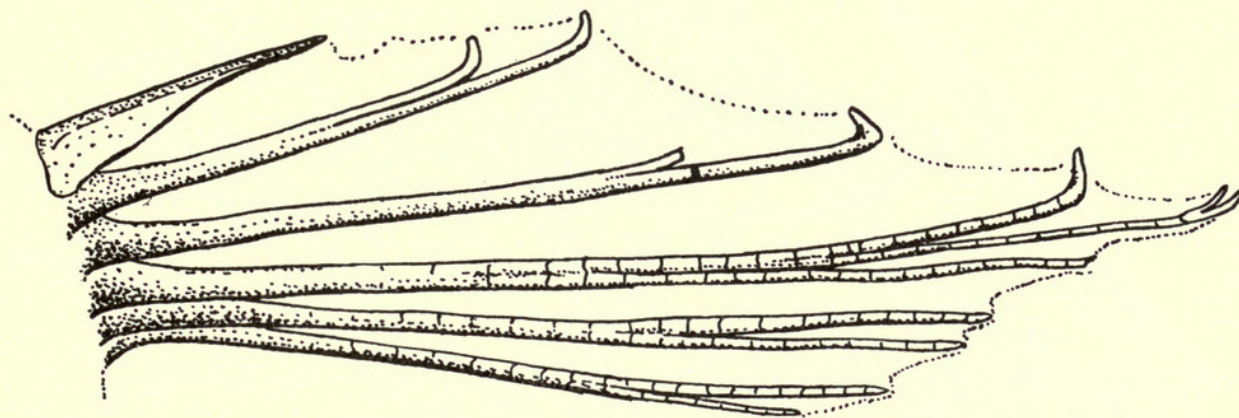

FIG. 17. *Pantanodon podoxys*, male. Left pelvic fin, ventral view, showing hook-shaped tips to the first three branched rays. Second ray unsegmented, but signs of segmentation in third.

In the female specimens of *Pantanodon*, the six pelvic rays are perfectly normal. In the male paratype of *P. podoxys*, however, the tips of the rays are modified (Text-fig. 17). The first short ray is spiny and terminates in a point ; the second and third rays, which are branched (the second without segmentation), have hooked, pointed tips directed laterally ; the fourth and longest ray is clearly segmented, and the two outermost branches have hooked tips (the innermost branch is damaged in all cases) ; the fifth and sixth rays are normal and branched.

A thickened, spiny first pelvic ray, and the hooked tips of the second and third rays, appear to be features which are unique amongst the toothcarps. Since they are confined to the male their function may possibly be concerned with some aspect of reproductive behaviour. The only other case of a thickened spine that I know of is in *Jordanella florida* which has a spinous first dorsal ; here the spine is clearly a double unit (i.e. split longitudinally) whereas in *P. podoxys* it is a single unit.

Axial Skeleton

In the two alizarin preparations of *P. podoxys* there are 29 vertebrae, of which 19 are caudal. Of the precaudal vertebrae, the first is without ribs or epiplurals, the next nine bear ribs, and seven of these also bear simple epiplurals also. The first caudal vertebra has an expanded haemal arch, but this is not found in any of the subsequent vertebrae.
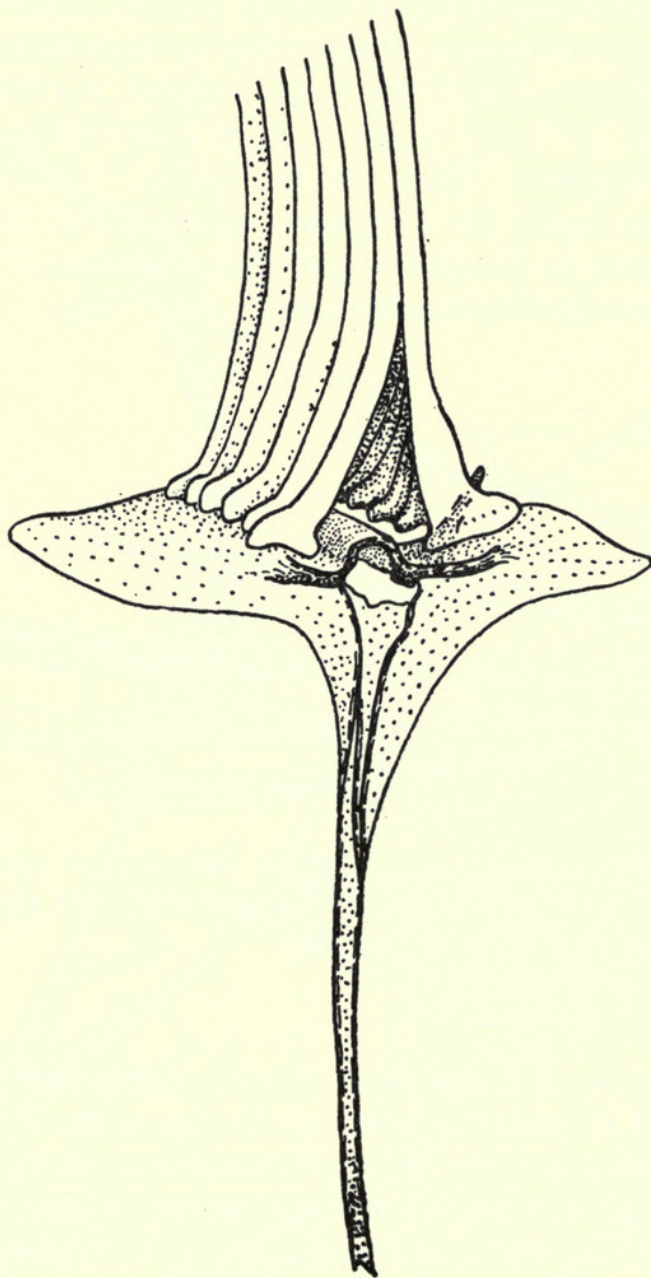

FIG. 18. *Pantanodon podoxys*. Pelvic girdle, right side, ventral view, from a female 17 mm. S.L.

This vertebral formula is little different from that found in other African cyprinodonts, but there seem to be rather more caudal vertebrae in *Pantanodon*. In *Procatopus nototaenia* there are 11–12 + 17 vertebrae, 12 + 16 in *Aplocheilichthys spilauchena*, and 11 + 17 in *Micropanchax loati*. In all of these the first vertebra bears an epiplural (but no rib). In *Pantanodon*, only in the first caudal vertebra is the haemal arch expanded, resembling the condition found in *Procatopus* (one, two or three),

Micropanchax (one), and *Aplocheilichthys spilauchena* (two) ; it should be stated, however, that it is not always possible to decide what are elongated parapophyses, and what are short ribs. But *Pantanodon* in no way approaches the condition found in *Epiplatys sexfasciatus* in which up to nine haemal arches are expanded.

The Caudal Skeleton (Text-fig. 19)

The caudal skeleton is shown in Text-fig. 19. The terminology used here is that of Gosline (1960), who preferred the use of " terminal vertebra " instead of " urostyle "
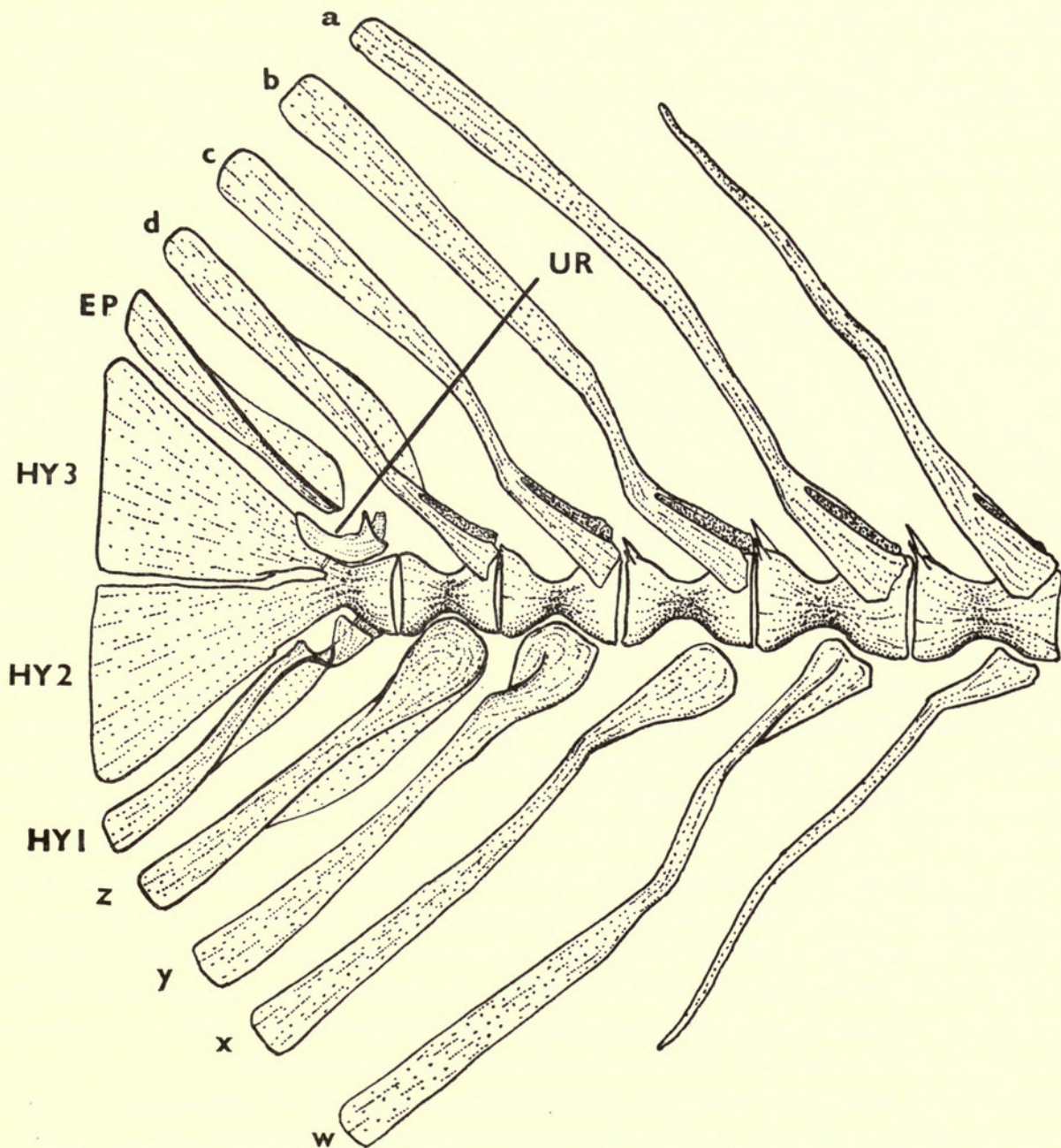
FIG. 19. *Pantanodon podoxys.* Caudal skeleton, from an alizarin stained specimen 17 mm. S.L.
            HY 1, 2 and 3. Hypural rays.
            EP. Epural.
            UR. Uroneural.
            a–d. Neural spines directly concerned with caudal support.
            w–z. Haemal spines directly concerned with caudal support.

in describing the posteriormost vertebra and the one with which the lowermost and laterally flanged hypural articulates. In *Pantanodon* the terminal vertebra is broadly conical with an upturned end, but there is little indication of the line of demarcation between the posterior border of the terminal vertebra and the base of the median hypurals. There is a small and perhaps paired uroneural (*UR*) lying above the terminal vertebra and overlapping the base of the uppermost hypural. There are three hypurals. The lowest (*Hy* 1 in Text-fig. 19) is a narrow bone which has a slight expansion along its antero-posterior face, and at each side near its base there is a lateral flange with posterolateral muscle attachments. Hypurals 2 and 3 are triangular and similar in shape and size. There is no indication that either is composed of several fused elements. Above hypural 3 there is a single, narrow epural (*EP*), similar in shape to hypural 1 but without an expanded base. The ultimate neural and haemal spines are expanded along their anterior faces into thin wings, and the blades of the last four neural and haemal spines are broader than those of the spines anterior to them (*a–d, w–z*). The posterior four spines reach the bases of the caudal rays and raylets, the spines on preterminal vertebra 4 (i.e. spines *a* and *w*) being rather elongated in order to do this.

The separation of hypurals 2 and 3 is well marked in *Pantanodon* and does not appear liable to subsequent fusion in larger fishes, although Hollister (1940) has shown that a tendency for this exists in certain viviparous toothcarps. In a specimen of *Epiplatys sexfasciatus* of 45 mm., however, the division is still complete, whereas in *Procatopus nototaenia* at 28 mm. there is a small split anteriorly, but posteriorly the median hypurals are fused. The hypurals are also split in *Aplocheilichthys spilauchena* and *Apolocheilus panchax*, but no separation of these hypurals was found in *Pachypanchax playfairii* (30 mm.) or in *Aplocheilichthys pelagicus* (40 mm.). Thus this character is not apparently stable amongst the Rivulinae or Procatopodinae, and it cannot be used for subfamilial relationships. Hollister (*loc. cit.*) shows a totally split median hypural in *Mollienesia sphenops*, a partial (anterior) median split in *Gambusia holbrooki* and juveniles of *Lebistes reticulatus*, and completely fused bones in adults of the latter and in *Fundulus bermudae*. In no case, however, does hypural 1 appear to either split or fuse, but in a specimen of *Aplocheilus panchax*, hypural 3 is split—perhaps an individual variant.

In three of the genera examined (*Epiplatys, Pachypanchax* and *Aplocheilichthys*) usually only the last three neural and haemal spines are concerned in the support of the caudal rays and raylets ; *Pantanodon* differs from these in its elongated fourth from last haemal and neural spines, which contributes to its deep caudal peduncle. In *Aplocheilichthys spilauchena* also, four spines support the caudal, while in *Aplocheilus panchax* only two neural and three haemal spines are concerned.

Uroneurals are not easy to distinguish in larger alizarin preparations, but they appear to be present also in *Procatopus, Aplocheilus* and *Aplocheilichthys*, but could not be seen in *Epiplatys*.

Apart from the small differences mentioned, the caudal skeleton of *Pantanodon* differs little from the other three genera, or indeed from the poeciliids described by Hollister (*loc. cit.*). Although fusion of the hypurals and the fate of the uroneurals may provide evidence of evolutionary progress at ordinal level (Gosline, 1960), the

variations in the toothcarps examined probably cannot be placed in phyletic series, but represent small variations on a rather similar general plan. In certain amblyopsoids, however, Gosline (1961) shows a rather different caudal pattern, hypural 1 having apparently lost all basal attachment, and hypural 3 being fused with a post-terminal vertebrae. I have found no post-terminal vertebra in any of the specimens already mentioned, nor any indication that they have become fused during ontogeny.

Pseudobranchiae

In *Pantanodon* there are no pseudobranchiae. Pseudobranchiae are not present in the Procatopodinae (or in the Fundulinae) but are found in the Rivulinae, and in these three subfamilies at least, their presence or absence is coupled with the presence or absence of vomerine teeth. The absence of vomerine teeth in *Pantanodon* may, however, represent a recent specialisation connected with feeding habits.

Habitat

I have no further data for the Tanganyika specimens beyond " in swampy land a few miles inland from Dar es Salaam." The Kenya fishes were caught in a ¼ acre salt-evaporating pool, one of a series built in lowlying, swampy land near enough to the sea to be flooded at high spring tides. Nearby are similar natural pools leading to a mangrove swamp, while inland there is a freshwater swamp and the large Sabaki (Athi) river. The lower Sabaki was intensively studied by the author and the only toothcarps discovered were species which had been introduced for malaria control. The pool in which *Pantanodon* was found contained also juveniles of some marine species, together with a runted population of *Tilapia mossambica*, a species well-known to tolerate saline conditions. The salinity of the pool at the time was approximately 40 parts per mille.

DISCUSSION

All too often in this paper it has been necessary to curtail discussion on the relationship of *Pantanodon* to other oviparous Cyprinodontidae owing to the lack of comparable studies on a particular feature. However, even the limited material on which comparisons have been made has indicated several relatively unexplored paths which should be followed up in a full revision of this section of the toothcarps. But since familial, let alone generic or specific descriptions and definitions, are in many instances inadequate, it has been possible here only to suggest *Pantanodon's* possible affinities, the more so because specialisation in *Pantanodon* has affected several useful key characters. It would seem, however, that *Pantanodon* is most nearly related to the Procatopodinae, although this subfamily is only barely represented in East Africa.

There is no reason to suppose that *Pantanodon* is a primitive form, but rather that it is a highly specialised genus which has evolved beyond the presently defined limits of the Procatopodinae. Neither is it an annectant form between the procatopodins and the rivulins. Zoogeographically, *Pantanodon* may represent a relic of a once widespread fauna common to both the eastern and the western watersheds of Africa. It has been suggested elsewhere (Whitehead in press) that the rivers of the eastern watershed of Africa may contain elements of an archaic fish fauna which became

isolated from the fauna of the west prior to the spread (in the west) of the many genera now associated with the Nile-Chad-Niger and Congo systems. But whereas the other cyprinodont genera in eastern Africa do not seem to have diverged greatly, *Pantanodon* does not have a counterpart in the west. It may perhaps have become adapted to a niche filled by other filter-feeders in the faunistically richer waters of the west.

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