

FOSSIL DENTICIPITID FISHES FROM
EAST AFRICA



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By P. H. GREENWOOD

SYNOPSIS

Recently, a new and distinctive family of small and primitive isospondylous fishes (Denticipitidae) was described from a living population in West Africa. Fossil representatives of this family have now been found in presumed Tertiary deposits near Mahenge, Tanganyika Territory. The living and fossil fishes are closely related but generically distinct; a new and monotypic genus (*Palaeodenticeps tanganyikae*) is created for the fossils. Other fish remains, predominantly Cichlidae, from the same deposits are described and discussed.

INTRODUCTION

SOME months ago I was asked to study a collection of fossil fishes from Mahenge in the Singida district of Tanganyika Territory. The age of the deposits is unknown but judging from some of the fishes present, it is probably of middle to late Tertiary age. This conclusion is in accordance with geological evidence from the sediments in which the specimens were found (Dr. G. Mannard, *in litt.*).

Amongst the fishes were a number of small specimens whose identity was a complete puzzle except that they were clearly Isospondyli of a clupeoid type. Various characters especially the denticulate cranial bones appeared to be unique and precluded the identification of the fishes with any known family of living or extinct Isospondyli.

This dilemma was solved recently by the publication of a paper describing a new family, Denticipitidae, of extant but primitive clupeoid fishes from rivers in western Nigeria (Clausen, 1959). The degree of resemblance between these fishes and the fossils is so remarkably close, that what differences there are can only be considered of generic value.

MATERIAL

The fossils are in the form of imprints left in lacustrine shales which have preserved the finest details of bone form and ornamentation.

Eight specimens are referable to the Denticipitidae, the majority being entire or almost entire skeletons still naturally articulated. Only one specimen is disarticulated and dispersed, although all have the posterior part of the skull somewhat crushed. The registration numbers given throughout are those of the Department of Palaeontology, British Museum (Nat. Hist.).

(1) Entire skeleton, well preserved. Standard length, 28 mm., total length (measured from snout tip to the posterior tip of the upper caudal lobe) about 32 mm. Holotype of the species: P. 42610.

(2) Entire skeleton, well preserved. S.L., 28 mm., T.L. 32 mm. Although the finer osteological detail is less obvious in this specimen, there is a very clear imprint of the swim-bladder; also, the structure of the caudal fin skeleton is clearer than in (1). P. 42611.

(3) Distorted and incomplete skeleton. S. L. about 28 mm. P. 42612.

(4) A well-preserved and almost complete skeleton lacking the anterior region of the skull and part of the anal fin. S.L. about 28 mm. P. 42613.

(5) and (6) Two specimens, one on each face of a piece of shale; both are incomplete skeletons rather poorly preserved. P. 42614 and P. 42615.

(7) A very badly preserved but almost entire skeleton of a fish about 25 mm. S.L. P. 42616.

(8) Part of the trunk and caudal skeleton (including the dorsal and anal fins) from a fish about 25 mm. S.L.; moderately preserved. P. 42617.

The descriptions which follow are based mainly on specimens (1) and (2) but some additional data were obtained from (3) and (4). The study and interpretation of this material was greatly facilitated by the use of "Silastomer" casts which gave a positive mould of the negative impression. From these casts it is possible to determine the extent and distribution of the finest cranial denticulations, as well as many other delicate structures in the cranial and axial skeleton. I am greatly indebted to Messrs. M. J. Meade and H. K. Ward of the Department of Palaeontology for their skilful preparation of the casts.

THE FAMILY DENTICIPITIDAE

The most outstanding characteristic of the Denticipitidae is, as the name implies, the presence of numerous extra-oral denticles on most dermal skull bones, on the dorsal part of the secondary pectoral girdle and on the scales around the anterior end of the lateral line (see Clausen, 1959 and Text-fig. 1). As far as skull denticulation is concerned, almost complete similarity exists between the fossils and the living species *Denticeps clupeoides*. Compression of the hinder end of the skull in the fossils makes it impossible to determine the dorsal elements of the pectoral girdle series. Consequently, this region could not be studied.

The few and slight differences which do occur in the skull denticulation of the two forms are principally: (i) the presence in the fossils of denticles on the suboperculum and (ii) fewer tooth rows on the lateral face of the maxilla and mandible, there being one less row on each bone. However, since these points can be checked in only two specimens and because nothing is known about the variability of such characters in living fishes, the taxonomic value of these differences cannot be assessed.

Despite careful search I am unable to find denticles on any scale impression, but, as the impressions are weak this difference also should not be given undue importance.

More significant differences noted in the fossils are: fewer vertebrae (31 or 32 cf. 40 in *Denticeps*) and lateral line scales (32 or 33 cf. 37 or 38) dorsal fin arising above the origin of the anal (and not more posteriorly as in *Denticeps*); more principal branched caudal rays (20 cf. 18).

These differences are slight when compared with the otherwise great similarity

that exists between every verifiable osteological character in the two forms. Unfortunately, the nature of the impressions precludes the study of median structures in the cranium (especially the relation between the supraoccipitals and parietals, and the shape of the nasal and parietal bones) nor is it possible to investigate the nature of the auditory fenestra. The large posttemporal foramen in *Denticeps* does appear to be developed in the fossils and is visible despite compression and distortion.

Clausen (1959) lays particular emphasis on the unique opercular lateral line system of *Denticeps*. The operculum carries from five to seven major sensory canals derived

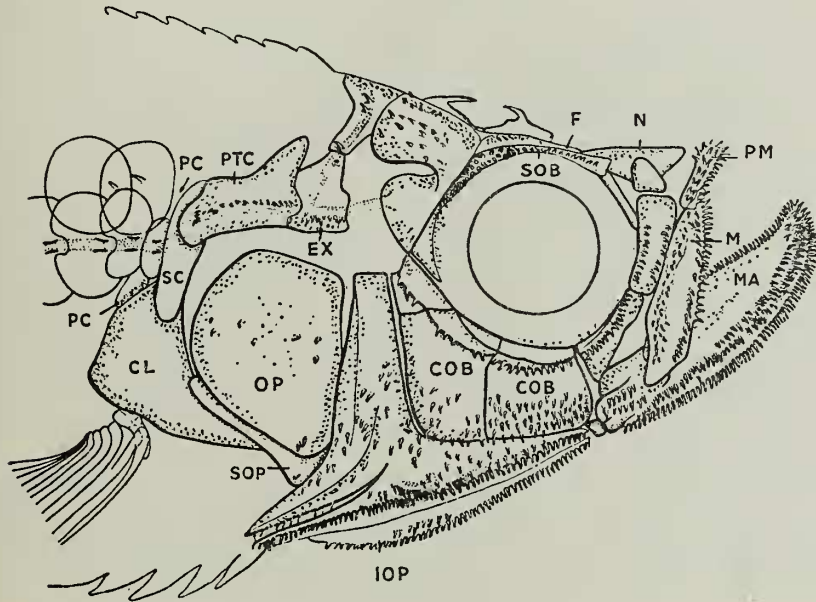


FIG 1. *Denticeps clupeoides* Clausen

Drawing of the syncranium and associated structures showing the superficial bones and the distribution of the dermal denticles; prepared from an alizarin specimen. In fresh specimens the denticles on the operculum and on the scales are more numerous. (After Clausen, 1959.) For abbreviations, see Text-fig. 2.

from the posttemporal-extrascapular and infraorbital-preopercular branches of the head. The canals are superficial, uncovered by bone and run obliquely across the bone in a postero-ventral direction. Each canal is fringed by rows of teeth. Naturally, such delicate structures are not well-preserved in the fossils. Nevertheless I believe that in two specimens the course of these canals is faintly visible. In these specimens there are two large toothed areas on the operculum, one situated dorsally and the other, larger area, occupying the antero-ventral angle of the bone (see Pl. 2). In both areas the teeth are arranged in orderly and approximately parallel lines running obliquely downwards and backwards; the lower group slopes less steeply

than the upper. The position and distribution of these teeth correspond to those fringing the canals in *Denticeps*.

Both *Denticeps* and the fossils have virtually identical caudal skeletons; as Clausen remarks, the caudal fin must be described as hemi-homocercal. A peculiar feature of the caudal is the presence of a comb-like group of three or four short, unbranched and detached rays which immediately precede the upper and lower caudal lobes. Laterally, the rays are supported by a band of narrow scales. The fossils show this character very clearly (see Pl. 3). The one difference I can find in the caudal skeleton is that only the last two vertebrae are curved upwards in the fossils whereas in *Denticeps* the last four to six vertebrae are involved. Finer details in the caudal osteology of the fossils are not easily discernible, but from observations on three specimens I should doubt whether a distinct urostyle is developed; the last vertebra is short and compact, and the ultimate uroneural does not extend beyond its posterior limits. Clausen (1959) mentions a urostyle in *Denticeps* but from his photograph of the caudal skeleton in an alizarin preparation, the situation would appear identical with that of the fossils.

One other familial character may be noted here, namely the postcleithrum. In *Denticeps* there are upper and lower postcleithra, both resembling dermal body scales and lying mesially to the shoulder girdle; the upper postcleithrum is pierced by the main lateral line tube. It is impossible to give a detailed description of the postcleithrum in the fossils because it is largely obscured by the cleithrum; only the ventral part is visible as a long, slender and postero-ventrally directed rod lying mesially to the cleithrum. No fine details are preserved and any dorsal relations with the lateral line system are obliterated by the crushed posterior part of the skull and upper girdle elements.

Considering the differences known to exist between the fossil and living Denticipidae, it seems reasonable to recognize the former as a separate genus. Certainly, when equated with the differentiae used in classifying present-day African fishes, these differences cannot be considered to have more than generic value.

Genus *PALAEODENTICEPS* nov.

DIAGNOSIS. A member of the family Denticipitidae, differing from the extant genus *Denticeps* in having fewer vertebrae (31 or 32 cf. 40) and lateral line scales (32 or 33 cf. 37 or 38); origin of dorsal fin above or slightly anterior to first anal fin ray, suboperculum with numerous small denticles, caudal fin with 20 (cf. 18) principal branched rays.

TYPE SPECIES. *P. tanganikae* sp. nov.

Palaeodenticeps tanganikae sp. nov.

(Pl. 1-3; Text-fig. 2)

DIAGNOSIS. As for the genus.

HOLOTYPE. A specimen about 28 mm. standard length. P. 42610.

LOCALITY. Lacustrine shales near the western margin of the Iramba Plateau, Singida district, Tanganika Territory.

AGE. Uncertain but probably middle to late Tertiary.

DESCRIPTION. In general appearance, *Palaeodenticeps* bears a striking resemblance to *Denticeps*. This overall similarity extends to a number of osteological characters (see above).

The scales along the dorsal mid-line form a clearly demarcated ridge and there is a distinct line of keeled scutes along the belly; about twenty scutes, extending from the level of the posterior preopercular margin to a short distance from the anal fin, form this ventral keel. The first ten pairs of ribs are intimately united with the scutes but the last three pairs are apparently free ventrally.

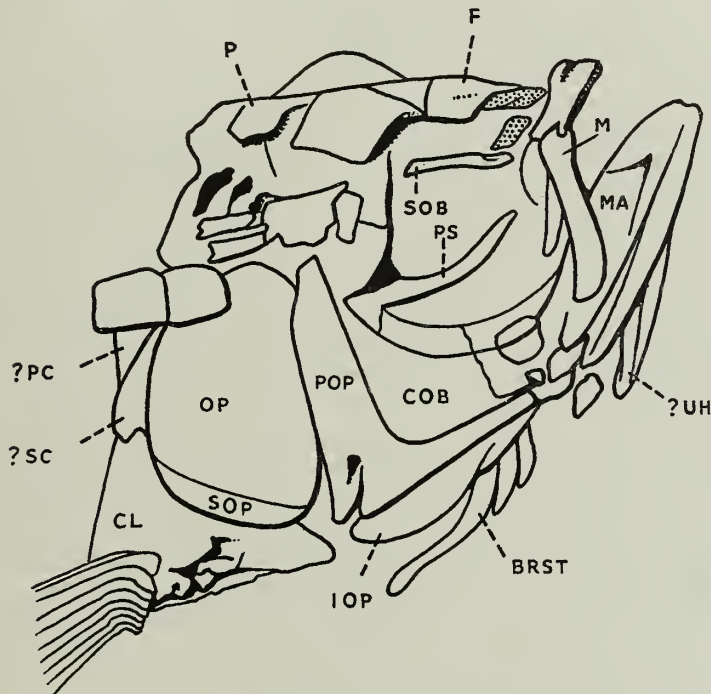


FIG. 2. *Palaeodenticeps tanganikae* sp. nov. Outline drawing of the syncranium, from the holotype ($\times 10$). P. 42610.

BRST., branchiostegal rays; CL., cleithrum; COB., circumorbitals; EX., extra-scapula; F., frontal; IOP., interoperculum; M., maxilla; N., nasal; OP., operculum; P., parietal; PC., postcleithrum; PM., premaxilla; POP., preoperculum; PS., parasphenoid; PT., posttemporal; SC., supracleithrum; SOB., supraorbital; SOP., suboperculum; ?UH., urohyhal (?)

As in *Denticeps*, the postero-ventral angle of the preoperculum is divided and forms a double projection fringed with denticles. Slightly posterior to the base of the division, there is a round depression which resembles an opening to the lateral line tube. No such pore is mentioned or figured in the description of *Denticeps*. The divided angle of the preoperculum is not markedly protracted in *Palaeodenticeps*;

in *Denticeps* it forms a double spine extending to a point below the posterior margin of the operculum (cf. Text-fig. 1 and Plate 2). Possibly, the spinous portion has been broken off in the fossils.

As mentioned above, the suboperculum carries scattered denticles. The interoperculum, like that of *Denticeps*, is toothed and pointed posteriorly; it appears to be stouter in *Palaeodenticeps* than in the extant genus. There are four or five, broad and stout branchiostegal rays; it is impossible to ascertain whether, as in *Denticeps*, the median pair is toothed.

No obvious differences could be detected in the circumorbital series of the two genera; the conspicuous, comb-like supraorbital of *Denticeps* does seem to be present in the fossils but this point needs confirmation.

In general, the lateral aspects of the pectoral girdle are alike in both genera but it is still unknown whether, as in *Denticeps*, there are two rows of pectoral radialis in *Palaeodenticeps*. The fin itself occupies a similar position, but the tip extends relatively more posteriorly in *Palaeodenticeps* where it reaches to the level of the ventral fin origin; there are nine pectoral rays in this genus. The ventral fins are poorly preserved in all the specimens and it is impossible to count the number of rays, except in so far as there are at least five and probably not more than eight.

The lateral line canal of the flanks is complete and extends from behind the cleithrum to the extremity of the caudal peduncle. It follows a gently curved course, situated midway between the dorsal and ventral body outlines. There are 32 or 33 scales in the lateral line series (counted in two specimens).

Apart from the total number of vertebrae and the number of up-turned vertebrae involved in the caudal fin skeleton (see above) there is little difference between the axial skeletons of the two genera. Faint traces of epineural and epicentral bones can be detected in two specimens, but the evidence for the presence of epipleurals is less definite. Dorso-spinal bones (i.e. elements apparently homologous with the dorsal pterygiophores but not bearing fin rays) are present above each of at least the first twelve vertebrae (that is, two more than in *Denticeps*).

The anal fin is long and low, comprising 24 or 25 branched rays; in the two specimens with entire anals there are three unbranched, unsegmented spine-like rays preceding the branched rays, thus giving a total fin ray count of 27 and 28. The dorsal fin is short and comprises eight rays (counted in three specimens); the first ray may be unbranched but apart from this possibility and its greater length, it is in no way different from the others. In some specimens, the branched parts of the dorsal rays appear to be very pliable and almost filamentous (judging from the way in which the distal ends of the rays have been thrown into curves). Other specimens seem to have more rigid tips to the dorsal rays, but this may merely be due to the vagaries of preservation.

One specimen (P. 42611) is particularly well preserved with little distortion or disarticulation. From this fish I have made a number of measurements, tabulated below. The fixed points used to obtain these measurements are, as far as possible, those used by Clausen (1959) to describe *Denticeps clupeioides*. Exceptions are marked with an asterisk (taken from the anterior tip of the premaxilla and *not* the mid-point of the upper jaw between the premaxillae); those marked with a dagger

are taken from the lateral end of the premaxilla and thus accord with Clausen's practice.

	mm.	% S.L.
Standard length	28.0	—
†Length of head	6.0	21.5
Depth of body	9.0	32.2
†Length of snout	1.3	4.7
Length of orbit	3.0	10.7
Postorbital head length	3.0	10.7
*Snout to 1st dorsal ray	17.0	60.8
†Snout to 1st anal ray	17.5	62.5
†Snout to pectoral insertion	6.0	21.4
†Snout to pelvic insertion	13.0	46.5
Pectoral to pelvic insertions	7.0	25.0
Length of dorsal fin at base	3.0	10.7
Length of anal fin at base	8.0	28.6
Caudal peduncle : $\frac{\text{Length}}{\text{Depth}}$	5.0	17.8
	4.0	14.3

ECOLOGY

Dr. G. W. Mannard of McGill University, who is studying the Singida deposits, has kindly informed me of his preliminary conclusions. He writes "These sediments are lacustrine shales which fill a depression in an area of granite near the western margin of the Iramba Plateau of central Tanganyika. The structure and heavy mineral content of the shales suggest that they are crater lake deposits over a kimberlite pipe". If *Palaeodenticeps tanganyikae* inhabited crater lakes, then its ecology differed considerably from the extant *Denticeps clupeioides*. This species is fluviatile and occurs in "fast-running, medium-sized streams of low mineral content" (Clausen, 1959). However, the ecological evidence for the fossils is too scanty to be considered conclusive, especially since the evidence furnished by associated fishes (see below) neither confirms nor contradicts it.

DISCUSSION

The Denticipitidae, both living and fossil, provide an intriguing puzzle. Clausen (1959) considers the relationships of the family with various isospondylous families and finds characters in common with the Elopidae, Albulidae and Clupeidae (all of the suborder Clupeioidi) as well as with Osteoglossidae (Osteoglossoidi). In addition, there are characters not found in any of these families or either suborder, as, for example, the denticulate dermal bones of the head. Indeed, the only other fishes with such extensive extra-oral cephalic dentition are those of the genus *Atherion* (Atherinidae, Mugiloidei, see Rofen, 1958), which are phylogenetically far removed from the Denticipitidae. As Dr. Clausen is still studying the anatomy of *Denticeps* I am unwilling to carry this discussion further. It must suffice to say that wherever the relevant characters are preserved in the fossils I have been able to confirm most of his observations; from Clausen's

published account and my own observations I would suspect that the Denticipitidae represent a group of subordinal status within the Isospondyli.

The known distribution of the family, with the fossil genus in the east (Tanganyika) and the extant *Denticiceps* in the west (Nigeria), is unusual; no other family of African freshwater fishes is restricted to such widely isolated areas. Further collecting may show that the living forms have a wider distribution and thus narrow the present geographical gap. Nevertheless the Denticipitidae do provide additional support for the concept of a once widespread, possibly pan-African, and relatively uniform ichthyofauna during the late Tertiary and early Quaternary periods. Evidence already available (Greenwood, 1951, 1959) shows that this was the condition over a relatively restricted area in East Africa where today there are at least three distinct faunal units.

THE FISH-FAUNA ASSOCIATED WITH *PALAEODENTICEPS*

At least two other families are present in the Singida collection. One of these is unidentifiable from the impressions preserved. The fishes represented are moderately large; one almost complete vertebral column is from a fish about 10 cm. long. Other unidentifiable material consists of isolated vertebrae, ribs and fin rays. None of these specimens is as well preserved as the *Palaeodenticeps* specimens or those of the other and identifiable family, the Cichlidae.

Thirteen specimens, all negative impressions and all referable to the same genus can be identified as cichlids (P. 42602-09 and P. 42618-22). Unfortunately, no entire skeletons are preserved, but from various fragments it has been possible to reconstruct several of the more important taxonomic characters.

The Cichlidae are widespread in Africa, and represented by numerous genera and species notorious for their complex and often difficult taxonomy. The really trenchant generic characters are found in the cranial osteology and in the pharyngeal dentition. None of these characters is preserved in the fossils so it has been necessary to rely on secondary characters such as scale types, number of vertebrae, fin ray counts and the oral dentition.

In a few specimens there are clear impressions of relatively stout and unicuspid teeth on the premaxilla and dentary; the teeth are not numerous in either jaw. Where scale impressions are present it is obvious that the scales are ctenoid. Taken together, these characters virtually eliminate the possibility of these fishes being *Tilapia*, one of the genera likely to be present in this region.

The low number of vertebrae (about 28) and the number of dorsal fin rays (15 spines + 9 branched rays) also reduced the possibility of these specimens being *Tilapia*. The sum of these characters, on the other hand, strongly suggests the genus *Haplochromis*, an ubiquitous genus distributed throughout Africa. The same characters, together with the general facies of the few almost entire specimens suggest close affinities with the extant *H. bloyeti* (Sauv.) and *H. wingati* (Blgr.), especially the former. The resemblance is not exact, but because of the difficulties in differentiating species of living *Haplochromis* I do not consider that any advantage would accrue from describing the fossils as a distinct species. *Haplochromis bloyeti* (which

occurs in the streams and rivers of present-day Tanganyika) has a wide ecological tolerance, as have most of the living generalized and fluviatile species. It would not be unreasonable to assume the same characteristics for the earlier species, which cannot therefore provide any critical information on the ecological conditions at the time preceding their death.

The earliest record of fossil Cichlidae in Africa is from Miocene deposits on Rusinga Island in Lake Victoria (Greenwood, 1951). Fishes from these beds share some characters with those from Singida, notably the small size, similar fin ray counts and a low number of vertebrae. Since the teeth and scales of the Rusinga fishes were not well preserved no generic identification could be made with certainty. Although I suggested that these fishes might be *Tilapia* (Greenwood, 1951), further material examined by Dr. Ethelwynn Trewavas indicates that some could be referred to *Haplochromis* or even to *Pelmatochromis* on the characters preserved (Trewavas, 1957, unpublished report). The identity of the Singida cichlids is certainly more definite.

ACKNOWLEDGMENTS

It is with great pleasure that I thank Dr. G. W. Mannard and Dr. H. S. Clausen who have discussed with me their unpublished researches on, respectively, the deposits and the living fishes; my thanks are also due to Dr. E. I. White, Keeper of Palaeontology, who read and criticized the manuscript of this paper.

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