Exploration du Parc National Albert

MISSION J. de HEINZELIN de BRAUCOURT (1950)

FASCICULE 4

Exploratie van het Nationaal Albert Park

ZENDING J. de HEINZELIN de BRAUCOURT (1950)

AFLEVERING 4

1. **QUATERNARY FISH-FOSSILS,**
   by P. H. GREENWOOD (Jinja, Uganda).

2. **OISEAUX FOSSILES,** par RENÉ VERHEYEN (Bruxelles).

3. **MAMMIFÈRES FOSSILES,** par A. TINDELL HOPWOOD (Londres)
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QUATERNARY FISH-FOSSILS

BY

P. H. GREENWOOD

INTRODUCTION

Fish-remains collected from deposits at Ishango (Lake Edward) and the Semliki valley by Dr. J. DE HEINZELIN's 1950 expedition, have increased considerably our historical knowledge of East African fishes. The collections are of especial value since their temporal range extends over the entire Pleistocene period, a time when the great lakes of Africa were undergoing extensive topographical changes and their faunae were subject to the vicissitudes of changing climate and hydrography. Indeed, the Pleistocene may be looked upon as a critical phase in the evolution of the present-day East African fish-fauna from an earlier and possibly pan-African type.

Many taxonomists and evolutionists have been attracted by the biogeographical problems which these lakes present. But, attempts to explain the often curious distribution of families and genera within the area have been hampered by the lack of an adequate palaeontological background.

The previous, often scanty, fossil records for the major lakes, Edward, Victoria and Albert, have provided tantalizing glimpses of the Tertiary and early Quaternary fishes living in the different basins. It was known, for instance, that during early Pleistocene times certain species now locally extinct, inhabited the Edward basin (WORTHINGTON, 1932; FUCHS, 1934). Likewise, in Lake Victoria there are records of the local extinction of *Tilapia nigra* during the lower Pleistocene and, going further back in time to the Miocene, the presence of two Nilotic genera, *Lates* and *Polypterus* for which there are no further records in the Victoria basin (TREWAVAS, 1937; GREENWOOD, 1951). In Lake Albert, on the other hand, there appears to have been little change in the major elements of the fish fauna since the lower Pleistocene (WHITE, *et al.* 1926).

Despite their importance, the significance of these discoveries was weakened by their isolation. The more complete record provided by the DE HEINZELIN collection enables these earlier discoveries to be seen in truer perspective and provides, for the first time, an account of one lake basin throughout a major period of its existence.

The brief description of the site, which preceeds the account of the fishes therefrom, is taken from notes supplied by the I.P.N.C.B. I have also given, in parenthesis, the number of the page in DE HEINZELIN's paper, « Le Fossé Tectonique sous le Parallèle d'Ishango » (1955), on which the site is described in detail.

ACKNOWLEDGEMENTS.

SITE I

K a n y a t s i, northern shore of Lake Edward, to the east of Ishango. B e d s   o f   K a i s o   a g e (p. 84); the fossils dislodged and washed amongst the pebbles of the beach.

DIPNOI

Fam. LEPIDOSIRENIDAE.

Protopterus sp.

One palatopterygoid and one splenial tooth-plate, probably derived from the same individual, are the only specimens of *Protopterus* from this site. Both tooth-plates are somewhat weathered, the upper being better preserved and more complete than the lower.

Neither specimen departs significantly from comparable tooth-plates of *P. aethiopicus*. It must be stressed, however, that only slight inter-specific differences exist in the tooth-plates of the four extant *Protopterus* species and that these differences are easily obscured by intra-specific variability and by wear. Thus, it would be unwise to attempt the specific diagnosis of these fossils on the basis of tooth morphology alone.

OSTARIOPHYSI

Fam. CHARACIDAE.

Hydrocyon sp.

This genus is represented by ten well-preserved teeth, all from large fishes. The enamel is discoloured a soft blue-grey.

Height of individual teeth (measured directly from base to tip) in millimetres : *ca.* 13; *ca.* 14; *ca.* 15(f3); 16; 17(f2); 18; 19 mm.

SILUROIDEA

Fam. BAGRIDAE.

Bagrus sp.

Bagrus is fairly well represented by the following material :

N e u r o c r a n i u m. — (i) An almost complete occiput derived from a skull about 23 cm long. This specimen comprises that part of the neurocranium slightly posterior to the frontal-supraoccipital suture; the lateral horn of the pterotic is wanting on both sides. As far as can be determined, the position of the sutures and of the exoccipital foramina are identical with those of *Bagrus docmac* (FORSKAL).

(ii) A large fragment of flat bone is thought to be part of a frontal. If this identification is correct, then the bone is from a skull greater than 25 cm neurocranial length.

(iii) An almost entire dermethmoid from a neurocranium about 14 cm long.

D e n t a r y. — Two fragments.

O p e r c u l u m. — A very small fragment comprising the facet and bone immediately surrounding it; from a skull of *ca.* 12 cm neurocranial length.

V e r t e b r a e. — The anterior fused vertebral mass is represented by two incomplete specimens, in which only the centra are preserved; estimated to be from fishes of *ca.* 24 and *ca.* 12 cm neurocranial length.

Clarotes sp.

The articular heads of twelve pectoral spines (1 left and 2 right) are assigned to this genus. Three other spine heads and three distal fragments are tentatively assigned to *Clarotes*.

Auchenoglanis sp.

Four fragments of neurocranium are referred to *Auchenoglanis* on the basis of their ornamentation, curvature and relative thickness.

The proximal part of a right pectoral spine can definitely be assigned to *Auchenoglanis*, as can an almost entire dorsal spine and the proximal part of another. Two incomplete pectoral spines (left and right) and two distal fragments of dorsal spines are tentatively referred to this genus. All specimens are from large fishes.

BAGRIDAE, GENERA INDETERMINABLE.

V e r t e b r a e . — One, somewhat damaged specimen of a 1st. vertebra (from a fish *ca.* 160 cm standard length); the centra of five precaudal and two caudal vertebrae (from fishes of *ca.* 145 and 160 cm standard length).

C l e i t h r u m . — A fragment from the slightly bullate region which overlies the articular fossa for the pectoral spine; perhaps nearest that of *Clarotes*.

S p i n e s . — The damaged articular heads of eleven pectoral spines.

Fam. MOCHOCIDAE.

? Synodontis.

This genus is probably represented by the following specimens : the proximal part of a pectoral spine whose articular head is damaged (from a fish *ca.* 30 cm S.L.); a fragment from the distal third of a dorsal spine and a fragment from the middle third of a pectoral spine (both from fishes about 35 cm S.L.).

More doubtfully referred to *Synodontis* are eight fragments of dorsal and pectoral spines.

Fam. CLARIIDAE.

? Clarias.

Two precaudal vertebrae (centra only) are tentatively consigned to this family and to the genus *Clarias*. It is estimated that the vertebrae are from fishes of *ca.* 60 and 75 cm. S.L.

FAMILY INDETERMINABLE.

Nine pectoral spines, all incomplete, and forty-two fragments from the distal ends of dorsal and pectoral spines are clearly derived from Siluroid fishes, but cannot be further identified.

S k u l l f r a g m e n t s (possibly *Clariidae*). — These pieces of roofing bones are too small for accurate identification; all are ornamented with low, blunt tubercles. No specimen shows any curvature, thus reducing the possibility of their being from *Auchenoglanis*, whilst the lack of ridges on the ornamented surface reduces the likelihood of their being from any known Bagrid.

PERCOMORPHI

Fam. CENTROPOMIDAE.

Lates cf. L. niloticus.

Specimens of *Lates* predominate, both numerically and in the diversity of elements preserved, over all other fish-fossils from this site.

Few interspecific differences can be detected in the skeletons of the extant species (or sub-species) *Lates niloticus* (LINNÉ), *L. albertianus* WORTHINGTON and *L. macrophthalmus* WORTHINGTON. Furthermore, where the fossils have been compared with these species no obvious differences could be determined. It is therefore impossible to assign the Kanyatsi material to any one of these species. Since WORTHINGTON (1940) is of the opinion that *L. albertianus* and *L. macrophthalmus* may be only sub-specifically distinct from *L. niloticus*, it would seem reasonable to consider this material as representing a lower Pleistocene population of *L. niloticus* which inhabited the Lake Edward basin.

N e u r o c r a n i u m . — (i) An almost entire neurocranium, the left side of which is more damaged and distorted than the right. Sinistrally the roofing bones are almost entirely absent, whilst dextrally these bones are virtually complete, although the supra-occipital and parietal ridges are broken. Likewise, the otic region of the left side is fractured and many of its elements displaced. Posteriorly, the median supra-occipital projection and the mesial exoccipital roof to the foramen magnum are both missing; the basioccipital facet is only slightly damaged.

Anteriorly, the skull lacks its ethmoid, pre-frontals and vomer. Since the parasphenoid terminates somewhat posteriorly to its junction with the vomer, it is impossible to measure the complete basilar length of this skull: the length taken from the anterior fracture to the most posterior point of the basioccipital facet is 25.7 cm; the estimated total basilar length is *ca.* 34 cm.

(ii) A fragment of neurocranium (from a large fish) comprises the dorsal roofing bones of the left otic region together with a small part of the sphenotic-pterotic lateral wall. The section of skull preserved is that between the posterior epiotic tip and the anterior extremity of the supra-occipital, which is sub-bisected, and with only the most anterior part of its spine present. The fragment measures 13 cm along this line.

Ethmoid-vomer region. — Seven specimens. With one exception most of the dermethmoid, parethmoid and the prefontals are preserved in each specimen. In the exceptional specimen, the parethmoid and prefrontal are present on one side only.

The smallest specimen is from a fish having an estimated neurocranial length (anterior vomerine tip to the basioccipital facet) of ca. 27 cm; the largest is from a skull at least twice that length.

The fossils differ only slightly from the ethmoid-vomer region of extant *Lates* species in that the vomerine tooth patch has the outline of a slightly rounded diamond, except in the largest specimen where it is approximately cardiform. This latter shape is that most frequently observed in extant species, irrespective of size.

Length of the vomerine tooth-patch is given as an indication of size. Due to its cardiform toothed area, the *largest* specimen appears somewhat smaller than the next largest specimen. Length of vomerine patch in cm : 2.5; 2.8; ca. 3.0; 3.3; 3.5; 4.4; 3.7.

The vomer alone is represented by nine specimens; their sizes (as measured above) are; 2.0; 2.2; 2.4; 2.5; ca. 2.7; 3.5; 3.6; ca. 3.3 and 3.2 cm.

There is also a single specimen comprising the dermethmoid, prefrontals and a small fragment of the frontals. It is estimated to be derived from a fish with a neurocranial length of ca. 27 cm.

Basiocciptal. — Represented by twelve specimens all showing remarkably similar lines of fracture : *ie.* the specimens comprise that area immediately posterior to the facet and the ventral portion of the bone. With three exceptions, all specimens exhibit a similar degree of mineralization and weathering. Exceptional specimens are more heavily mineralized and badly weathered; in addition, the first vertebra is preserved *in situ.*

The size-range is indicated by the greatest width of the basioccipital facet. In those specimens with an associated first vertebra, width of the vertebral face is given; such specimens are indicated thus * : 2.8; 3.3; 3.1; 3.5; ca. 3.6; 4.0; 4.1; 4.1; 5.0; ca. 4.3*; 4.9*; and 5.1* cm.

Epiotic and parietal — A fragmentary specimen includes part of the epiotic-parietal suture and part of the lateral epiotic wall with its post-temporal suture.

Jaws.

Dentary. — Eighteen specimens (eleven right, seven left) none of which is entire. Since it is both difficult and misleading to estimate the total length of fishes from which such fragmentary specimens were derived, two measurements of the bone itself are given : its depth at the symphysis, and, the width of the dentigerous surface at its broadest point (where this point is preserved).

Symphysial depth (cm).	Greatest width (cm).
2.0	1.2
2.5	ca. 2.0
2.7	1.5
2.8	—
ca. 2.8	2.2
3.0	—
3.0	2.0
3.1	—
3.1	1.9
3.1	2.9
3.1	1.8
3.3	1.9
3.3	ca. 1.8
3.4	2.3
3.4	—
3.5	2.3
3.8	2.6
3.8	2.3

P r e m a x i l l a. — Eight specimens (4 left, 4 right), none entire. All are from the anterior half to third of the bone. Size range is indicated by breadth of toothed surface immediately adjacent to the symphysial surface : 3.1; 2.7(f2); 2.6; 2.5(f3); 2.3; and 1.4 cm.

In addition, there is a fragment from the middle portion of the premaxilla.

M a x i l l a. — Represented by only one large specimen (left) from the anterior half of this bone, but lacking the articular head.

Q u a d r a t e. — Twenty-six specimens (10 left, 16 right) all incomplete. In each, however, the facet is preserved, as are varying amounts of the posteriorly directed basal limb, the anterior ascending margin and the body of the bone. Excepting two small specimens, all were derived from large fishes. As an indication of size, breadth of the facet is given : 1.2; 1.5; 2.3; ca. 2.4; 2.5; 2.6; 2.8; 2.9 (f2); 3.0 (f3); 3.2; 3.3 (f3); 3.4; ca. 3.5 (f2); 3.5 (f2); ca. 3.6; 3.6 (f2); 3.7; and 3.9 cm.

Without exception, these specimens are heavily mineralized and somewhat weathered

A r t i c u l a r. — Seventeen fragmentary and variously fractured specimens (9 left, 8 right). In each, the entire or greater part of the articular head is preserved, and in some, part of the anterior limb as well.

No really satisfactory measurement can be used to indicate the size of fishes from which the specimens were derived; all are large, the largest probably from a skull ca. 55 cm basilar length, the smallest from a skull of ca. 27 cm. The modal size is only somewhat less than that of the largest bone.

P r e o p e r c u l u m. — A single specimen (left), almost entire and well preserved; thought to be from a skull of *ca.* 40 cm basilar length.

O p e r c u l u m. — Represented by a small fragment from the antero-dorsal angle of the bone.

E c t o p t e r y g o i d. — Four specimens (1 left, 3 right) of which two are almost entire. The two largest specimens are estimated to be from skulls of *ca.* 50 cm basilar length, the smaller bones are from skulls of *ca.* 35 and *ca.* 20 cm basilar length.

U r o h y a l. — Two specimens both fragments, from the anterior part of the bone. One specimen can be unequivocally identified as the urohyal of *Lates* but the other differs somewhat from both its fossil cogener and the urohyal of extant species. Its form is, however, nearer that of *Lates* than any other known genus.

V e r t e b r a e.

1 s t V e r t e b r a. — Eleven specimens. With one exception all show slight signs of weathering, particularly of the anterior articular surface; the exceptional vertebra is remarkably well-preserved. Greatest measurements of the centrum are given for : breadth across the anterior face, depth of the anterior face and length : 5.0, 4.1 and 2.5 (f3); 4.0, 3.2, 2.0 (f4); 3.2, 2.6 and 1.8 (f3); 1.8, 2.8, 1.2 (f1) cm.

2 n d V e r t e b r a. — Thirteen specimens. With one exception all lack the neural spine and prezygapophyses, and in some specimens the postzyga-pophyses are also missing. The exceptional vertebra retains the proximal third of its neural spine as well as both pairs of zygapophyses. The material exhibits a wide range of weathering.

Centrum measurements, taken as for the 1st vertebra, are : 5.6, 4.7 and 2.2 (f1); 4.7, 4.0 and 2.0 (f4); 3.5, 3.5 and 2.2 (f1); 3.0, 3.0 and 2.3 (f1); 2.7, 2.6 and 1.4 (f3); 2.1, 1.8 and 0.8 (f1); 1.8, 1.6 and 0.8 (f1). One specimen is too badly damaged for accurate measurement.

3 r d V e r t e b r a. — Twenty-four specimens, showing various degrees of weathering and preservation; none is entire. Centrum measurements taken as above : 5.5, 4.6 and 2.5 (f5); 5.0, 4.5 and 2.4 (f6); 4.5, 3.7 and 2.0 (f8); 4.0, 3.0 and 1.5 (f4); 3.7, 2.5 and 1.5 (f1) cm.

In addition, there is a specimen of vertebrae 3 and 4 preserved in articulation; centrum measurements (as above), taken from the 3rd vertebra, are 5.5, 4.5 and 2.8 cm.

4 t h V e r t e b r a. — One well-preserved and almost entire bone lacks only the distal half of its neural spine. Centrum measurements (as above) :

1.8, 1.6 and 1.3 cm. Two other fourth vertebrae are less well preserved and measure 3.7, 2.7 and 2.2 cm, and 3.5, 2.7 and 2.3 cm respectively.

Two specimens each comprise the 2nd-4th vertebrae still in articulation. Since the fourth vertebra in one group is damaged, measurements for this specimen are taken from the posterior face of the third vertebra : breadth 4.5, height *ca.*3.5, length 2.3 cm. In the other specimens, measurements taken from the posterior face of the fourth vertebra are : 5.5, 4.5 and 2.8 cm.

Other precaudal vertebrae.

Because characters serving to identify individually the fifth to eleventh vertebrae are not always trenchant, even when preserved, it is necessary to consider these elements grouped as 5th-7th; 8th-9th and 10th-11th vertebrae.

In most specimens the neutral spine is wanting, although the basal portion of the neural arch is sometimes present. Otherwise these bones are well preserved and have undergone only slight weathering.

Vertebrae 5-7. — Twenty-four specimens. Measurements are given for the breadth of the anterior face, depth of this face and the length of the centrum : 6.4, 4.7 and 6.5; 6.0, 4.5 and 4.5; 5.7, 4.4 and 4.0(f2), 5.5, 4.5 and 4.1 (f2); 5.4, 4.0 and 3.5; 5.3, 4.0 and 3.2; 5.2, 4.1 and 3.8; 4.8, 4.2 and 3.8; 4.8, 3.7 and 3.0; 4.7, *ca.* 3.6 and 3.2; 4.4, 3.5 and 3.0 (f2); 4.3, 3.5 and 3.0; 4.2, 3.8 and 3.0; 4.2, 3.3 and 3.3; 3.4, 3.0 and 2.8; 2.9, 2.2 and 2.0; 2.3, 2.0 and 1.9. One specimen is too badly damaged for even approximate measurement.

Vertebrae 8 and 9. — Sixteen specimens; measurements taken as above : — 6.0, 4.5 and 4.5 (f3); 5.2, 4.5 and 4.0 (f3); 4.5, 4.4 and 3.6 (f3); 4.3, 4.0 and 3.4(f1); 4.0, 3.7 and 3.2(f2); 3.6, 3.2 and 3.1(f1); 2.8, 2.8 and 2.6(f1); 1.8, 1.8 and 1.8 (f2) cm.

Vertebrae 10 and 11. — Twelve specimens; the centrum is damaged in five specimens and none has well preserved neural arches or lateral parapophyses. Measurements as above : — 6.4, 5.2 and 4.0; 6.0, 5.2 and 4.6 (f2); 4.8, 4.6 and 4.0 (f4); 4.0, 4.0 and 4.3; 3.5, 3.2 and 3.0 (f1, plus one damaged vertebra estimated to have these dimensions); 3.0, 3.0 and 2.5 (f1); 2.4, 2.4 and 2.4 (f1) cm.

Caudal vertebrae.

Forty-one specimens whose serial identity cannot be determined. The state of preservation and degree of weathering shown by these bones is comparable with that of the precaudal vertebrae, although a larger number of caudal elements has damaged centra. In only two specimens are the neural arches and spines preserved, and in none is the haemal arch present. Measurements (as above) are : — 5.0, 4.8 and 3.8 to 4.6, 4.2 and 4.0 (f7); 3.8,

4.2 and 3.4(f8); 3.6, 3.6 and 3.3(f1); 3.2, 3.5 and 2.5 to 3.0, 3.0 and 2.5(f14); 2.8, 2.8 and 2.6(f5); 2.6, 2.6 and 2.5 to 2.5, 2.5 and 2.0(f3); 2.0, 2.0 and 2.0(f2); 1.5, 1.5 and 1.9(f1) cm.

Penultimate and last vertebrae. — One specimen comprising both these elements in association. Another specimen is of the last vertebra only.

Other vertebrae. — The serial identity of twenty-seven vertebrae (and one fragment) cannot be determined; the majority are probably precaudal elements.

Pectoral girdle. — Represented by three fragmentary specimens of the *cleithrum*, which are, however, sufficiently characteristic to allow their immediate identification.

Fins.

Spines. — Thirty-eight specimens of various lengths, but including the proximal articular portion, are most probably dorsal fin-spines; the possibility that some may be anal spines cannot entirely be discounted. Two distal fragments are tentatively assigned to *Lates*.

Ten additional fragments should probably be referred to this genus.

Interneural and interhaemal pterygiophores: The distal ends of five interneurals, together with the proximal two-thirds of a sixth specimen are placed in this genus, as are four incomplete interhaemals.

Pectoral fin-rays. — Four articulated rays from the anterior part of the fin are assigned to *Lates*.

Pectoral spine. — A small fragment from the distal end of a spine should probably be referred to this genus.

Fam. CICHLIDAE.

Tilapia sp.

This species is very poorly represented by a caudal vertebra, lacking both neural and haemal arches (from a fish *ca.* 40 cm S.L.), and by distal portions of two interhaemal pterygiophores, from fishes of about the same size.

Since there are so few specimens of *Tilapia* from this site, and because the genus is not represented in other deposits of this age, the possibility that these specimens were derived from younger deposits cannot be overruled.

GENERICALLY INDETERMINABLE MATERIAL.

Fin-spines. — 6 fragments, one probably from a *Siluroid* fish and five from percomorphs.

Pterygiophore. — A fragment.

? Basioccipital. — A fragment probably from the basioccipital facet.

Dentigerous bones. — Two; one possibly a fragment of *Lates* pharyngeal bone, the other probably from the dentary of this species.

Of particular interest are two, small, sub-circular objects which cannot even definitely be considered as fish remains. Their smooth, almost polished exterior is suggestive of enamel and compares closely in texture and colour with the enamel surface of *Hydrocyon* teeth from this horizon. The presumed upper surface has the form of a low dome; the lower aspect is less regular in outline, with a narrow circular periphery enclosing a shallow, reddish-brown concavity. A distinct neck separates the curved upper surface from the narrow periphery of the lower surface. The greatest diameter of the two specimens is 0.65 and 0.5 cm, and the least diameter is 0.6 and 0.4 cm.

Since these objects are at present unidentifiable it is only possible to suggest that they may be pharyngeal teeth of some large fish, perhaps an extinct Cyprinid, or, as seems more probable, they may be parasphenoidal teeth from a large *Hyperopisus*-like fish.

SITE II

Kanyatsi. Beds of Kaiso age (p. 85). Fossils detatched by erosion and the trampling of animals.

OSTARIOPHYSI

SILUROIDEA

Fam. BAGRIDAE.

Siluroid fishes from this deposit are very poorly represented by fragments tentatively assigned to the Bagrid genera *Auchenoglanis* and *Clarotes*.

Auchenoglanis sp.

The proximal part of a pectoral spine, including the articular head, is referred to this genus on the basis of the detailed structure of its various articular surfaces.

Clarotes sp.

The damaged proximal ends of two pectoral spines are assigned to this genus. As in the spines refered to *Auchenoglanis*, few characters are preserved which will permit precise diagnosis. In neither of the *Clarotes* spines is the articular part entire, but the major head is fairly complete in both specimens.

A fragment of dentary is tentatively identified as that of *Clarotes*.

Fam. CLARIIDAE.

Two fragments of dentigerous bones are probably derived from Clariid fishes.

GENERICALLY INDETERMINABLE SILUROIDEA.

(i) A small and badly damaged pectoral spine fragment.

(ii) Part of a pectoral spine still associated with its matrix.

(iii) Three fragments of fin-spines.

PERCOMORPHI

Fam. CENTROPOMIDAE.

Lates cf. L. niloticus.

Neurocranium. — (i) Part of a skull comprising the entire right side of the basioccipital, the lower part of the exoccipital (including the greater part of its condyle), that portion of the opisthotic enclosed between the exoccipital, basioccipital and the parasphenoid, and the posterior part of the parasphenoid. An almost undamaged first vertebra is preserved *in situ.* Neurocranial length of the entire skull is estimated to be *ca.* 23 cm.

(ii) Basioccipital : two specimens, neither entire. Estimated to be from neurocrania *ca.* 25 and *ca.* 35 cm long.

(iii) Vomer : one incomplete specimen but including the dentigerous area, which is cardiform in outline; from a skull *ca.* 25 cm long.

(iv) Parasphenoid : six fragments of various sizes, representing portions from the preorbital region of this bone. All are derived from large fishes.

Jaws.

Dentary. — Six fragments (4 left, 2 right) from the anterior (symphysial) portion; all are from large fishes. As an indication of size, the vertical height at the symphysis is given : Left : 4.2; 3.9; 2.9; and 2.7 cm. Right : 3.5 and 3.1 cm.

Premaxilla. — A small fragment from the anterior half of the bone; derived from a large fish. Another, and even more fragmentary specimen is also derived from a large fish.

Articular. — Two badly damaged specimens (both right) each comprising the facet and region immediately surrounding it; both are derived from large fishes. The greatest length of the facet is 2.1 and 2.7 cm for the specimens respectively.

Quadrate. — A single fragmentary specimen. The greatest breadth of the articular surface is 1.8 cm.

Preoperculum. — (i) A large fragment which comprises the greater part of the vertical limb and a small portion of the horizontal limb. The characteristic spines at the lower angle are damaged, but the origin of the first two, ventrally directed spines is preserved. The estimated height of the vertical limb — taking its sensory canal openings as base — is 17 cm.

(ii) A small fragment from the lower part of a vertical limb, immediately above its point of curvature into the horizontal limb.

(iii) A somewhat smaller specimen, still associated with its matrix. This bone is no more complete than either specimen described above, but represents an entire horizontal limb with the three ventrally directed spines well preserved.

Pectoral girdle.

Cleithrum. — Represented by three specimens. (i) A fragment from the angle between vertical and horizontal limbs of the bone; derived from a very large fish.

(ii) A smaller fragment also from the same region.

(iii) A small fragment from the horizontal limb immediately anterior to the angle between horizontal and vertical limbs; from a very large fish.

? Supracleitrum — A single specimen, derived from a very large fish, is considered to be the proximal end of this bone.

Vertebrae.

Unless specified otherwise, all measurements of breadth and height were taken from the anterior face of the centrum.

First vertebra. — A well preserved and almost entire specimen, breadth 3.9; height 3.2 and length 2.3 cm; a fragment (the right half of the centrum), estimated breadth and length 6.5 and 3.5 cm respectively; a fragment comprising the right anterior facet and a small part of the centrum immediately below it, thought to be derived from a vertebra about 4 cm broad and 2.5 cm long.

Second vertebra. — Two specimens, one almost complete, the other lacking its neural arch and prezygapophyses; b.3.1, h.3.4 and l.1.6; 1.7, 1.7 and 0.8 cm respectively.

Third vertebra. — Four specimens, one of which is badly damaged. (i) b.6.4, h.4.9, 1.3.0 cm; (ii) 2.4, 1.8, 1.3 cm; (iii) 1.8, 1.5, 1.1 cm; no measurements were made on the fourth specimen.

Precaudal vertebra. — Five fragments of centra, three from large fishes and two from smaller individuals.

Caudal vertebrae. — Two almost complete specimens (b.3.3, h.2.9 and l.3.0 and 2.8, 2.8, 2.5 cm) and two fragments.

Fin-spines.

Four large fragments from the proximal ends of Percomorph fin-spines should probably be assigned to *Lates*. Two other fragments, from the distal end, are also referred to this genus but with less certainty.

INDETERMINABLE MATERIAL.

Fourteen fragments and three large specimens are undoubtedly of fish origin, but cannot be identified further.

SITE III

Katanda aval, Upper Semliki. Deposits of Kaiso age, extending some metres above the water and forming a small hill below the ford (pp. 43 and 46).

OSTARIOPHYSI

SILUROIDEA

Fam. BAGRIDAE.

Clarotes sp.

Tentative identifications. — (i) The poorly preserved anterior region of a large skull is tentatively assigned to *Clarotes*. The specimen comprises the dermethmoid and part of the prefrontal of each side. Few diagnostic characters are preserved but the shape of the dermethmoid is nearest that of *Clarotes* and there are traces of *Clarotes*-like tubercles present on the posterior part of the prefrontal.

(ii) The anterior fused vertebral mass; a single specimen derived from a large fish. Almost the entire length of the fused centra is complete and a large part of the right lateral wing is present. The base of the median dorsal plate is preserved, as are the basal and lower portions of the paired and posterioly directed spines. As far as can be determined from this fragmentary and fragile specimen the morphology of the elements preserved is nearer that of the vertebral mass in *Clarotes* than in *Bagrus*.

A large and extensively damaged skull can be definitely assigned to *Clarotes*. Besides the neurocranium some elements of the branchiocranium and an almost entire pectoral girdle are preserved *in situ*. The whole structure has undergone dorso-ventral compression so that the hyomandibulae, pterygoids and operculae are displaced laterally. The hyoid arch is less affected, whilst the pectoral girdle is apparently undistorted. Many bones are damaged, especially on their superficial surfaces.

Neurocranium. — The exposed dorsal surface is rather fragmentary and none of the roofing bones is preserved in their entirety.

Ethmoid. — Only the left side of the ethmoid, and an almost complete left prefrontal are present. The tuberculate ornamentation on the ethmoid

is confined to its antero-medial aspects and is replaced postero-medially, and to a lesser degree laterally, by fairly well defined divergently radiating ridges.

V o m e r. — Part of the left vomerine tooth-band is visible on the under-surface of the skull.

F r o n t a l s. — Both frontals are incomplete. Although sutures cannot be determined with certainty, it seems probable that the anterior part of the left frontal and its union with the ethmoid of that side are preserved. The right frontal is present only in its posterior extension, including part of the junction with the sphenotic. The frontals bear numerous discrete tubercles which are not uniformly distributed but aggregated into posterior and lateral fields, separated by a zone of fine striations. Both the striae and the tubercles are arranged radiately.

Part of a deep fontanelle separating left and right frontals is preserved.

Neither sphenotic is present although there is a clearly defined outline impression of the right sphenotic.

None of the dorsal or dorso-lateral bones posterior to the frontals is preserved on the left side of the neurocranium.

The right pterotic is almost complete although much of its dorsal surface is damaged. Where present, the ornamentation is tuberculate, with the tubercles smaller and more densely aggregated than those of the frontals and ethmoid. Laterally, the right hyomandibula lies in intimate contact with the pterotic.

The entire occipital region is wanting.

B r a n c h i o c r a n i u m.

H y o m a n d i b u l a e. — The greater part of both hyomandibulae is well preserved; the right hyomandibula is apparently in articulation with its pterotic facet.

The posterior part of the pterygoid is present on each side. Anteriorly, a small part of the forward end of the arch is visible below the left prefrontal. It is overlain by part of the somewhat laterally displaced palatine. Consequent upon this displacement, the dentigerous patch of the palatine is so orientated that it overlies and is continuous with the left vomerine tooth-band.

H y o i d   a r c h. — The slightly damaged epi-, cerato- and hypohyals of both sides, together with their median basihyal are preserved *in situ*. These bones are displaced laterally to a degree comparable with the hyomandibulae and pterygoids.

O p e r c u l a e. — The entire right operculum is preserved and the left is represented by an almost complete outline impression. Ornamentation

of the right operculum takes the form of numerous distinct and narrow ridges radiating centrifugally from a focus near the facet.

J a w s .

P r e m a x i l l a e   a n d   D e n t a r i e s . — Nearly the entire left premaxilla is preserved in approximately its natural position; only a median fragment of the right premaxilla remains. The left dentary is represented by its antero-median portion, and the right merely by its symphysial head.

P e c t o r a l   g i r d l e . — This massive structure is only slightly damaged. The lateral surfaces of the cleithra are strongly ornamented with large, well-spaced tubercles; the slight swellings which overlie the articular fossae for the pectoral spines are ornamented with several vertical and sub-parallel ridges. On each side, the heads and proximal ends of the pectoral spines are preserved in articulation; because the exposed surfaces are badly weathered, it is impossible to determine the nature of any ornamentation which might have been present on the spines.

Fragments of both post-temporals are still associated with their respective cleithra.

Within the limits imposed by its fragmentary nature, this specimen is comparable in size and general appearance with a skull described by ARAMBOURG (1947) from the Omo Beds of Lake Rudolf. ARAMBOURG refered his specimen to *Clarotes laticeps*, but I do not consider the Ishango specimen to be sufficiently well-preserved to warrant specific identification.

Only four measurements can be estimated with any accuracy.

Length (measured from the anterior ethmoidal mid-point to the posterior margin of the pterotic) : *ca.* 30 cm.

Greatest breadth (taken across the hyomandibulae heads after « restoring » them to their natural position) : *ca.* 18 cm.

Length of right sphenotic (taken along its lateral margin) : *ca.* 8 cm.

Greatest length of right pterotic : *ca.* 10 cm.

GENERICALLY INDETERMINABLE MATERIAL.

V e r t e b r a e . — A number of anterior abdominal vertebrae, apparently derived from one individual, is preserved within a lump of matrix. Several vertebrae are still arranged serially, whilst others, more anterior in the series, are displaced. These bones are very similar to comparable elements in the vertebral column of *Bagrus*, to which genus they are tentatively assigned.

UNIDENTIFIABLE MATERIAL.

Twenty fragments and impressions of bones, some of which are only doubtfully considered to be of fish origin.

SITE IV

K a s a k a, f a c e à S e n g a, Upper Semliki. K a i s o b e d s, outcropping about 15-20 metres above the water, and situated on the left bank of the Semliki, slightly before the junction of Semliki and Kasaka rivers (pp. 40-41). Fossils freed by erosion and by the trampling of animals.

OSTARIOPHYSI

SILUROIDEA

Fam. BAGRIDAE.

GENUS INDETERMINABLE.

V e r t e b r a e. — One anterior precaudal vertebra (from a large fish) which compares closely with serially equivalent vertebrae in *Bagrus*. Centrum measurements, taken from the anterior face, are : breadth *ca.* 3.4, height 3.7 and length 1.6 cm.

P e c t o r a l s p i n e s. — Two damaged specimens; in each the articular head and proximal third of the spine are preserved. Because of their poor preservation, these specimens are assigned only tentatively to the *Bagridae.*

Fam. MOCHOCIDAE.

Synodontis sp.

Four fragments of dorsal spines are referred to this genus, as are two fragments thought to be derived from pectoral spines.

FAMILY INDETERMINABLE.

Two very fragmentary pectoral spines probably should be assigned to the *Bagridae.*

One fragment from the proximal end of a dorsal spine closely resembles this spine in extant *Auchenoglanis occidentalis*, especially with regard to its coarse sculpturing.

PERCOMORPHI

Fam. CENTROPOMIDAE.

Lates sp.

One, well-preserved gill-raker from the epibranchial of arch I can definitely be referred to this genus. Length : *ca.* 4.7 cm. (Measured from the basal mid-point to the distal tip).

Ten fragments of fin-rays should probably be assigned to *Lates*.

INDETERMINABLE MATERIAL.

Three large fragments (probably parts of the parasphenoid) representing at least two genera, together with five smaller fragments also of neuro-cranial origin, cannot be identified further.

SITE IV a

Between Ishango and Kanyatsi (point fossilifère L. 273 et L. 352) about 40 metres above the lake.

OSTARIOPHYSI

Fam. CHARACIDAE.

Hydrocyon sp.

This genus is represented by three, well-preserved teeth. Height of teeth (measured directly from base to tip) in millimetres *ca.* 15.0, 15.3 and 19.0.

PERCOMORPHI

Fam. CENTROPOMIDAE.

Lates sp.

Two large (length of each centrum *ca.* 5 cm) and almost complete centra of abdominal vertebrae, with a fragment from a third, preserved *in situ*; five other vertebrae (4 abdominal and 1 caudal) and one vertebral fragment. A fragment of fin spine should probably be referred to this genus.

SITE V

S e n g a, Upper Semliki. K a i s o b e d s outcropping about 10-15 metres above the water. Situated on the right bank, somewhat below the rapids and the junction of the Semliki and Kasaka rivers (p. 37). Fossils freed by erosion and by the trampling of animals.

OSTARIOPHYSI

SILUROIDEA

Fam. BAGRIDAE.

? Auchenoglanis sp.

The material listed below is tentatively referred to *Auchenoglanis* since trenchant diagnostic characters are not present in any specimen. Identification is on the basis of greater correspondence with comparable structures in *Auchenoglanis* than in any other extant Siluroid genus. The specimens comprise :

(i) The posterior part of the basioccipital, including its facet; derived from a fish with a neurocranial length greater than 16 cm (the largest *A. occidentalis* available to me). The facet measures 3.1 cm in breadth and is 3.1 cm high.

(ii) A neurocranial fragment whose curvature and ornamentation agree closely with certain bones in the skull of *A. occidentalis*; also derived from a large fish.

(iii) A left humeral process and postero-lateral part of the cleithrum; from a fish as large as that, or those, from which specimens (i) and (ii) originated.

(iv) Part of the proximal two-thirds of a large pectoral spine.

PERCOMORPHI

Fam. CENTROPOMIDAE.

Lates sp.

The genus is poorly represented by the following specimens :

1st Vertebra. — Rather weathered and possibly somewhat compressed; from a large fish. Depth (posterior face of the centrum) 5.2, breadth (anterior face) 5.7 and length 3.2 cm.

Posterior precaudal vertebra. — A well-preserved but incomplete specimen : Breadth (anterior face) 2.8, height (anterior face) 2.7 and length 2.6 cm.

Preoperculum. — A fragment from the lower part of the vertical limb; estimated to be derived from a fish about 100 cm standard length.

Quadrate. — A small fragment from the antero-ventral angle; derived from a large fish.

GENERICALLY INDETERMINABLE MATERIAL.

(i) A small bone, possibly part of the proximal end of a Siluroid pectoral spine.

(ii) Four fragments, of uncertain origin.

SITE VI

Katanda amont, Upper Semliki. Beds of the Semliki Series (Middle Pleistocene), situated on the right bank, about 23 metres above the water (p. 47).

Fish remains from this site are few in number and very fragmentary. In most cases, generic identification is problematical.

OSTARIOPHYSI

SILUROIDEA

CLARIIDAE. — A fragment of neurocranium has ornamentation closely approximating that of present-day *Clarias*. An anterior precaudal vertebra is also referred to this genus (breadth 2.9 cm, height 2.8 cm [both from the anterior face of the centrum] and length 0.9 cm).

BAGRIDAE. — Three fragments of flat bone with coarse, tuberculate ornamentation are tentatively referred to this family. They may represent species of *Clarotes* or *Chrysichthys*.

? MOCHOCIDAE (*? Synodontis*). — Represented by the proximal part of a fin-spine estimated to be derived from a fish about 20 cm standard length.

Unidentifiable material. — Four fragments of bone.

In addition to this material Dr. DE HEINZELIN has kindly sent me a few further specimens collected by him in 1954.

These specimens are identified as follows :

CLARIIDAE (*Clarias* sp.). — A fragment of neurocranium.

? BAGRIDAE. — Four fragments of neurocranium should probably be referred to this family, although their ornamentation is coarser than that seen in extant *Clarotes* and *Chrysichthys*.

Additional material collected from this site in 1954 (27-30 m above the river) :

Synodontis : fragment of pectoral spine.

Lates : a fragment of vertebra (and possibly one other fragment).

SITE VII

As for site VI, except that the fossils were collected from a dispersed outcrop (p. 47).

Only three fish-fossils can be identified with certainty.

OSTARIOPHYSI

CYPRINOIDEA

CYPRINIDAE (*Barbus* sp.). — Represented by the crown of the largest tooth in the pharyngeal series; derived from a fish *ca.* 75 cm standard length.

SILUROIDEA

CLARIIDAE. — The posterior half of a left dentary (from a fish *ca.* 60 cm standard length) is referred to the genus *Clarias*.

Generically Indeterminable material. — A small fragment of thin, curved bone, probably from the rim of a centrum.

SITE VIII*a*

I s h a n g o G. I N F., at the source of the Semliki. Excavations.
Debris derived from ancient formations (t h e m a j o r i t y f r o m K a i s o
b e d s). The bones black, heavy and rolled.

DIPNOI

Fam. LEPIDOSIRENIDAE.

Protopterus sp.

The only specimen of *Protopterus* from this deposit is an incomplete,
and heavily rolled, left dentary and splenial tooth-plate.

This splenial tooth-plate differs slightly from those of extant *Protopterus*
species which I have examined, or, for which figures are available. The
principal difference lies in the fossil possessing a deep, medially directed
depression which separates the low, continuous inner ridge from the third
(posterior) outer ridge. In *P. aethiopicus* these two ridges run imperceptibly
into oneanother. Nothing indicates that the depression in the fossil is due
to wear or *post-mortem* damage.

A less obvious difference is that the third ridge is short in relation to the
total length of the tooth-plate. The validity of this ratio is perhaps doubtful,
since in *P. aethiopicus* it shows some size correlated variation, with the third
ridge longer in large fishes.

The entire tooth-ridge, measured over its long axis from the posterior
edge to the symphysial surface, is 5.3 cm long.

OSTARIOPHYSI

SILUROIDEA

Fam. CLARIIDAE.

Eight fragments of sculptured neurocranial bones are placed in this
family on the basis of their ornamentation. They should probably be
referred to the genus *Clarias*.

Fam. MOCHOCIDAE.

.Synodontis sp.

One specimen only, (the articular head and proximal quarter of a pectoral spine) is referred to this genus. The relatively slight degree of weathering shown by the spine is in marked contrast to the other, heavily weathered specimens from this deposit.

Fam. BAGRIDAE.

Clarotes sp.

Two incomplete pectoral fin spines (left and right) are assigned to this species. Two damaged pectoral spines (both right), together with the proximal end of a third specimen, and two distal fragments are tentatively referred to *Clarotes*.

SILUROIDEA, FAMILY INDETERMINABLE.

Four fragments of dentigerous bones.

PERCOMORPHI

Fam. CENTROPOMIDAE.

Lates sp.

Vertebrae provide the only evidence for the presence of *Lates* in this deposit. All specimens are somewhat rolled.

F i r s t   v e r t e b r a. — One specimen, from a large fish. Measurements taken from the posterior face are : breadth 4.4, height 4.5, length 3.3 cm.

T h i r d   v e r t e b r a. — One, damaged specimen : breadth 3.4 and length 1.7 cm.

F o u r t h   v e r t e b r a. — Four specimens whose measurements (taken from the anterior face) are : (i) b. 3.9, h. 2.0, l. 3.1 cm; (ii) estimated to be about the same size as (i) but split obliquely across its long axis; (iii) b. 3.9, h. 2.0, l. 3.1 cm; (iv) b. 2.7, h. 1.1, l. 2.0 cm.

A badly damaged vertebra is identified as a posterior precaudal element.

There are also two anterior caudal vertebrae (measurements as above) : (i) b. 2.8, h. 3.0, l. 2.5 cm; (ii) b. 1.7, h. 1.7, l. 1.6 cm, and one face of a large vertebra whose greatest and least diameters are 6.6 and 6.0 cm respectively.

SITE VIII*b*

As for VIII *a*, but the debris probably autochthonous; trench N 143ᴳ E, G. INF.; lower level of the Ishango terrace (Epi-Pleistocene). Bones light-brown to dark brown in colour, relatively light, porous and little rolled.

OSTARIOPHYSI

SILUROIDEA

Fam. BAGRIDAE.

Clarotes sp.

The articular heads of two pectoral spines (1 left, 1 right) are referred to this genus.

Fam. MOCHOCIDAE.

Synodontis sp.

The genus is represented only by a number of incomplete fin-spines identified as follows :

D o r s a l   s p i n e. — Three specimens all from fishes of about 25 cm standard length.

P e c t o r a l   s p i n e. — Six specimens (three from the proximal end [1 left, 2 right] and three from the distal end of the spine); derived from fishes between 18 and 30 cm standard length.

SILUROIDEA, FAMILY INDETERMINABLE.

Part of a dorsal fin-spine.

CYPRINOIDEA

Fam. CYPRINIDAE.

Barbus sp.

Material referred to this genus comprises one vertebra (from a fish about 40 cm standard length) and, less certainly, part of the third (ossified) dorsal ray.

PERCOMORPHI

Fam. CENTROPOMIDAE.

Lates sp.

Three caudal vertebrae, from fishes of *ca.* 65-70 cm standard length.

Fam. CICHLIDAE.

Tilapia sp.

P r e c a u d a l   v e r t e b r a e. — Five specimens, one from a fish of *ca.* 40 cm. standard length and four from individuals of *ca.* 35 cm.

F i r s t   i n t e r n e u r a l   p t e r y g i o p h o r e. — One, the articular surface only; from a fish of 45-50 cm standard length.

F i n   s p i n e s.

A n a l   s p i n e. — One; this stout and short spine is probably the second anal spine from a fish of *ca.* 45-50 cm standard length.

D o r s a l   s p i n e s. — One anterior spine, almost entire, and one other, more posterior in the series (from a fish or fishes of about 40 cm standard length). There is also a somewhat rotted fragment, probably from a dorsal spine.

P e c t o r a l   s p i n e. — One almost entire and well preserved spine, from a fish *ca.* 45 cm standard length.

GENERICALLY UNIDENTIFIABLE MATERIAL.

(i) a fin-spine; (ii) one vertebra; (iii) a fragment of bone, possibly not of fish origin.

SITE VIII c

As above, but trench N 43ᴳ E.

Material from this site is well preserved, shows few signs of weathering and is lightly mineralized. Consequently, it contrasts strongly with the heavily mineralized and weathered specimens of site VIII a, particularly with regard to the preservation of fine detail. In many respects, including the adherent micaceous matrix, the appearance of fossils from site VIII c closely resembles that of specimens from VIII b and from the Makalian deposits of site IX.

DIPNOI

Fam. LEPIDOSIRENIDAE.

Protopterus cf. P. aethiopicus.

Dentary and splenial tooth-plate. — Seven specimens (5 left and 2 right); the entire dentary is present in one specimen, the tooth-plate is complete or very nearly complete in three, and is represented by its anterior part in four other specimens. Two indications of size are given : first, for complete teeth, the length of the tooth-plate, and secondly, for incomplete plates, the height of the first tooth fold.

(i) 4.7, 4.0 and 4.2 cm; (ii) 1.4, 1.3, 1,2 (f2) cm.

Palatopterygoid tooth-plate. — One rather fragmentary specimen, in which the first and second tooth-ridges are preserved.

All these specimens are well-preserved; none shows any marked morphological differences from comparable tooth-plates in *Protopterus aethiopicus*.

OSTARIOPHYSI

SILUROIDEA

Fam. CHARACIDAE.

Clarias cf. C. lazera and Clarias cf. C. mossambicus.

The tentative specific identification is based on the surface sculpturing of the bones.

Clarias lazera. — One prefrontal (from a fish about 75 cm standard length); two ? post-temporals (from a fish of about 75 cm S.L.); *Clarias mossambicus* : two unidentifiable neurocranial bones.

Clarias sp. indet. — A fragment of parasphenoid.

Fam. MOCHOCIDAE.

Synodontis cf. S. frontosus.

Pectoral girdle. — The specific identification of the fish from which this bone was derived is based on the restored outline of the left humeral process and on the sculpturing visible on part of the process.

Two incomplete but well preserved pectoral spines are also referred to this genus.

PERCOMORPHI

Fam. CENTROPOMIDAE.

Lates sp.

Parasphenoid. — One large fragment.

Entopterygoid. — A small fragment from the posterior end of the bone.

Preoperculum. — Two specimens. One is a fragment from the angle of the bone. The other is more complete, but lacks the horizontal anterior limb and the proximal part of the vertical limb.

D e n t a r y. — One damaged specimen.

V e r t e b r a. — A specimen of the second vertebra, well preserved and lacking only the neural arch.

Except for the fragment of entopterygoid, all these bones were derived from fishes about 75 cm standard length. The entopterygoid is from a larger individual, probably about 85 cm standard length.

Fam. CICHLIDAE.

Tilapia sp.

Part of the operculum (the upper anterior angle and articular facet) estimated as being derived from a fish about 28 cm standard lenght.

SITE IX

I s h a n g o, source of the Semliki; the principal fossiliferous beds (N.F.PR.) of M a k a l i a n (E p i - P l e i s t o c e n e) age; (p. 65).

DIPNOI

Fam. LEPIDOSIRENIDAE.

Protopterus cf. P. aethiopicus.

Sixteen palatopterygoid tooth-plates are referred to *Protopterus aethio-picus*. There is, however, some variability which, although worthy of note, is still within the limits of individual variation as observed in living fishes.

Greatest departure from modal *Protopterus aethiopicus* tooth morphology is shown by the form of the ridge or hump which lies at the confluence of the second and third lateral tooth-ridges. In the extant material examined (six specimens) and in six of the fossils, this point is either a broad plateau or a short, broadly rounded ridge lying almost antero-posteriorly and at an obtuse angle to the second lateral ridge. In the remaining fossils it appears as a prominent, somewhat elongate peak almost equalling in size the first lateral tooth-ridge. Since hypertrophy of this inner ridge only

occurs in larger specimens its development is probably a function of overall body size, and its manifestation probably related to diet. Evidence for the latter supposition is provided by the teeth of *P. aethiopicus* from Lake Victoria. In this lake, the species feeds mainly on Mollusca and the tooth plates of large fishes show greater signs of attrition than are evident in the teeth of comparable sized or even larger fossil individuals.

The third, or posterior, lateral ridge exhibits great variation in its outline, which, although basically rhomboidal, may vary from an elongate to a short rhombus. This variation is not obviously correlated with size. In all the extant material examined the third ridge is clearly elongate, in fact, more so than in any fossil.

As in the young of living fishes, the cutting edge of the teeth in smaller specimens is serrated.

The splenial tooth plate is represented by nine incomplete specimens. None shows any marked departure from that of *Protopterus aethiopicus*. In addition there is a small fragment presumed to be derived from a splenial tooth.

The material represents fishes from *ca.* 50 to *ca.* 150 cm total length.

OSTARIOPHYSI

SILUROIDEA

Fam. CLARIIDAE.

Clarias cf. C. lazera and Clarias cf. C. mossambicus.

Nearly all the *Clarias* material from this site may be referred to species closely resembling *C. lazera* and *C. mossambicus*. The remaining specimens are without obvious diagnostic characters.

Comparison of the neurocrania of *Clarias lazera* and *C. mossambicus* shows that although most elements do not differ in their outline or spatial relationships, some may be differentiated specifically on the basis of their superficial ornamentation. Other slight but specifically constant differences were noted in the form of the sutural surfaces uniting the frontals.

The neurocranial elements preserved are :

D e r m e t h m o i d. — Thirty specimens with *Clarias lazera*-like ornamentation (tubercles more numerous, higher and more pointed), ten being almost entire and twenty from the anterior portion of the bone.

One, almost complete specimen is referred to *Clarias mossambicus*.

P r e f r o n t a l s. — *Clarias lazera* (more highly ornamentated, with finer, more numerous and discrete tubercles), left 57, right 17 specimens.

One prefrontal is tentatively referred to *Clarias mossambicus* and six others are considered specifically unidentifiable.

F r o n t a l s. — One character was determined for distinguishing between the frontals of *Clarias lazera* and *C. mossambicus*, namely the ornamentation (tubercles more numerous and discrete in *C. lazera*).

On the basis of this character the material is divided as follows :

Clarias lazera : 44 specimens (19 left, 24 right and one paired);

Clarias mossambicus : 2 specimens (left and right);

Clarias sp. indet. : 15 fragments.

None of these specimens is entire and the areas of the frontal represented by them are varied.

S u p r a o r b i t a l. — Only *Clarias lazera* is represented; the material comprises twenty-one fragments (15 left, 6 right), of which four are almost entire, thirteen are of the anterior third or less and four are from the middle third.

Three further fragments are tentatively identified as supraorbitals.

J u g a l. — *Clarias* sp.; three fairly complete bones (1 left, 2 right).

S u p r a o r b i t a l. — Two entire (right) and two almost entire bones (left and right) are assigned to *Clarias lazera* on the basis of their sculpturing.

S p h e n o t i c. — *Clarias* sp.; seven fragments only one of which is almost entire. Four other specimens are identified provisionally as pieces of *Clarias* sphenotic.

D e r m o s p h e n o t i c. — One nearly complete bone can be referred to *Clarias lazera*. The dermosphenotic in this species has its tubercles arranged in centrifugally radiate striae, whereas in *C. mossambicus* the tubercles are distributed more irregularly.

S u p r a o c c i p i t a l. — Twenty-two incomplete specimens; the majority from that part of the bone anterior to the fontanelle. The ornamentation is considered to be nearer that of *Clarias lazera* than *C. mossambicus*.

One fairly complete specimen is referred to *Clarias mossambicus*.

P t e r o t i c. — Eight fragments of pterotic are assigned to *Clarias lazera* because of their numerous, acute and densely arranged tubercles.

P o s t - t e m p o r a l. — Three fragments, which cannot be identified specifically. Two other fragments are though to be derived from the post-temporal of *Clarias*.

In addition to these identifiable neurocranial roofing bones, there are ninety-two fragments too small for accurate identification. Judging from the ornamentation of these bones, both *Clarias lazera* and *C. mossambicus* are represented, the former species predominating.

Two of the fragments represent a fish, or, fishes considerably larger than those from which the other fragments or more complete bones were derived. Both in their thickness and in possessing coarse, blunt tubercles, the exceptional fragments closely resemble Clariid neurocranial fragments found in lower gravel G. INF. at site VIII *a* (v i d e p. 27) and may be derived from older deposits.

P a r a s p h e n o i d. — The twenty-one fragments of parasphenoid can be divided into two groups of ten and eleven specimens each, representing the anterior and posterior halves of the bone respectively. No specific characters can be determined.

B a s i o c c i p i t a l. — Eight, almost entire bones.

V o m e r i n e t o o t h - b a n d. — A single fragment from the median part of the band, together with a splinter of the vomer itself.

The following elements of the branchiocranium were identified :

P a l a t i n e. — Seven specimens (four entire and three less than half complete).

H y o m a n d i b u l a. — Two fragments; derived from the postero-ventral aspect of the bone.

O p e r c u l u m. — Eight specimens, all more or less entire.

V e n t r a l e l e m e n t s o f t h e h y o i d a r c h. — It should be noted that any apparent differences which may exist between these elements in *Clarias mossambicus* and *C. lazera* are outweighed by intra-specific growth changes.

Left.

(i) Epihyal only : twenty specimens; the majority are broken at the epi-ceratohyal suture.

(ii) Ceratohyal only : twelve specimens, fractured as above.

(iii) Epihyal and ceratohyal : seven entire specimens.

(iv) Ceratohyal and hypohyal : one specimen.

Right.

(i) Epihyal only : nineteen specimens, mostly fractured as above.

(ii) Ceratohyal only : seven specimens, mostly fractured as above.

(iii) Epihyal and ceratohyal : one entire specimen.

U r o h y a l. — Sixty-three specimens; with two exceptions all these bones are well preserved.

Q u a d r a t e. — Thirty-four specimens (15 left, 19 right), none entire. Fracture lines are variable and no common breakage pattern can be detected.

A r t i c u l a r. — Sixty-five specimens (28 left, 37 right). The majority is virtually entire, lacking only the most anterior projection. In only one case is there a fragment of the dentary still closely applied by its lateral sutural union. Although there appear to be at least two species represented, it is obvious from a study of extant material that changes in form associated with growth are as great as the differences observed in the fossils.

D e n t a r y. — Fairly reliable characters for differentiating the dentary of *Clarias mossambicus* from that of *C. lazera* were determined from a study of the skeletons of these species. But, the criteria cannot be applied to the fossil material with any certainty.

There are ninety-five specimens in all, comprising forty-two left and fifty-three right rami. Two points of fracture are most frequent : (i) at or slightly behind the point where the dentigerous surface narrows laterally; (ii) immediately behind the most posterior extension of the dentigerous surface.

P e c t o r a l   g i r d l e. — Cleithrum.

(i) Median ventral portion : represented by forty-four fragments of various sizes (19 left, 17 right and 8 indeterminable). The marked striae and rugosities preserved in the fossils are nearer the ornamentation of *Clarias lazera* than of *C. mossambicus*.

(ii) Lateral portion (especially the enlarged area accommodating the articular fossae for the pectoral spine) : twenty-two specimens (13 left, 9 right). No trenchant diagnostic characters are preserved.

(iii) Scapula and coracoid : four large fragments of both elements in which the trochlea and glenoid facets are preserved, and three specimens comprising only the coracoid with part of the glenoid facet.

P e c t o r a l   s p i n e. — Twenty specimens (10 left, 10 right), eight of which are practically undamaged; the remainder comprise the proximal half to third of the spine. In all, the articular head is present and only slightly damaged.

Vertebral column.

Anterior fused vertebral mass. — Ten fragmentary specimens.

In general it is impossible to differentiate *Clarias lazera* from *C. mossambicus* on vertebral morphology.

1st Vertebra : seven.
2nd Vertebra : six.
3rd Vertebra : twelve.
4th Vertebra : seven.
5th-9th Vertebra : eighteen.

It is remarkable that amongst the great number of fish vertebrae recovered from this site, none can be unequivocally recognized as caudal vertebrae of *Clarias*.

Ribs. — Thirteen small, hamate bones are identified as pleural ribs of *Clarias*.

Size range and number of individuals.

The estimated size range of *Clarias lazera* from this deposit is 45-100 cm, with a modal range of 75-80 cm; few fishes less than 60 cm are represented. The minimum number of individuals present is estimated at 63 (the number of urohyal bones preserved).

? **Heterobranchus** sp.

With the exception of the vomerine tooth band and the dentary, the tentative generic identification of the specimens described below is based solely on characters of ornamentation.

In *Heterobranchus* the tuberculate ornamentation characteristic of many *Clarias* species is, to a large extent, replaced by radiating striae. This is particularly marked on the frontals, prefrontals and dermethmoid. When present, tubercles are of a type intermediate between those of *Clarias lazera* and *C. mossambicus*.

Frontal. — 8 fragments (5 left, 3 right).

Mesethmoid. — One fragment.

Lateral ethmoid. — Two fragments.

Sphenotic. — One fragment.

Post-temporal. — One fragment.

Supraoccipital. — A single fragment from the anterior end.

One unidentifiable fragment of roofing bone.

All these bones were derived from fishes of about 60 cm total length.

D e n t a r y . — A fragment from the posterior part of the bone.

V o m e r i n e t o o t h - b a n d . — A small segment from the median part of the band, together with a splinter of vomer, is referred to *Heterobranchus* on the basis of its shape and the small dental alveoli, which indicate that the teeth were slender. It was derived from a fish longer than 60 cm total length.

Fam. MOCHOCIDAE.

Synodontis spp.

The genus *Synodontis* does not occur in the present fish-fauna of Lake Edward and it is therefore of considerable importance to determine what species were present when the Epi-Pleistocene beds were laid down.

To this end, the fossils were compared with *Synodontis frontosus*, *S. schall*, *S. nigrita*, *S. victoriae* and *S. afro-fischeri*. These species were selected on the grounds of their present distribution as those most likely to have occured within the Lake Edward basin, assuming of course, that the species were already evolved at that time.

Sculpturing and ornamentation of neurocranial bones provide the most readily determined specific characters for fossil material which is often fragmentary. Additional criteria are provided by the shape and ornamentation of the humeral process, and, the morphology of the dorsal fin-spine.

These admittedly few and not altogether satisfactory characters suggest that most of the fossils may be referred to *Synodontis frontosus*, a species at present found in Lake Albert, the Nile, Lake Rudolf and Lake No. A few bones are apparently attributable to *S. schall*, whose present distribution is Lake Albert, the Nile and the Niger.

Although, in the characters examined, correspondence between fossils and extant fishes may not be exact, there is no reason to suppose that on morphological grounds the Ishango fishes represent an undescribed and presumably extinct species. The differences observed are matched by the observed intra-specific variability of living *Synodontis frontosus*.

The following bones were identified :

D e r m e t h m o i d . — Twenty-five specimens, of which twenty-one are almost entire.

P r e f r o n t a l . — Ten specimens (4 left, 6 right); all are entire or almost so.

F r o n t a l . — One hundred and forty-five specimens (59 left, 86 right), all referred to *Synodontis frontosus*; the majority is entire, or, virtually so. Most specimens exhibit a cancellous pattern underlying the superficial

tuberculate ornamentation. This deep pattern is considered to be an artifact resulting from partial decay and weathering of the bone before fossilization; it is present in most other *Synodontis* neurocranial bones from this site. Similar cancellous patterns were observed in the bones of extant *Synodontis* picked up as skeletons on the shore of Lake Rudolf, but are absent in skeletons prepared from fresh or preserved material.

S p h e n o t i c. — Nineteen specimens, mostly entire.

S u p r a o c c i p i t a l. — Sixty-two specimens.

P o s t - t e m p o r a l. — Thirteen specimens (8 left, 5 right).

O c c i p i t o - n u c h a l   p l a t e :

(i) Anterior unpaired plate : one almost entire bone and sixteen fragments (11 left, 5 right) of various sizes; all have ornamentation of the *Synodontis frontosus*-type
Two small fragments are tentatively identified as anterior nuchal plates.

(ii) Postero-lateral paired plates : three specimens (2 left, 1 right) are also referred to *Synodontis frontosus*.

Forty-eight skull bones (neurocranial and probably some nuchal-plate elements) cannot be identified. All have ornamentation approximating to that of *Synodontis frontosus*.

B a s i o c c i p i t a l. — Four entire specimens, three of which compare closely with the basioccipital in *Synodontis frontosus;* and the fourth (derived from a large fish) is more like that of *S. schall*.

P e c t o r a l   g i r d l e.

C l e i t h r u m   a n d   h u m e r a l   p r o c e s s. — On hundred and fifteen specimens (58 left, 57 right); with few exceptions, the lateral, dome-like expansion of the cleithrum and the greater part of the ascending limb are preserved. A large area of the humeral process is present in many specimens.
The ornamentation of these bones is similar to that of *Synodontis frontosus* Further, in many specimens the humeral process is almost complete, or it is sufficiently complete to allow the reconstruction of its posterior outline. In this character too, the fossils resemble *S. frontosus*, in which the length/depth ratio of the humeral process is approximately unity.
One hundred and fifty (62 left, 88 right) fragments, mostly of the lateral dome or the ascending cleithral limb, cannot be specifically identified.
Only two specimens (one left and one right but from different individuals) are tentatively referred to *Synodontis schall*. In these two bones the lower margin of the humeral process has a predominantly striate pattern and an approximate reconstruction of their outline indicates that the humeral process was longer than deep.

Coracoid. — Four fragments (1 left, 3 right) and in addition, a large fragment from the horizontal, median expansion of the bone.

Pectoral spine. — No trenchant specific characters were observed in the pectoral spines of the extant species examined; the fossils are therefore considered as specifically indeterminable.

Right spine. — Sixty-seven specimens, of which thirty-three are entire, or, two-thirds entire, nine have at least the proximal third intact and twenty-four have less than the proximal third preserved. One specimen has only the distal two-thirds preserved. The articular head is preserved in all but five spines.

Left spine. — Eighty-one specimens, comprising thirty-three complete, or, two-thirds complete, twenty-eight with at least the proximal third present and twenty with less than the proximal third intact. With one exception the articular head is present in each specimen.

Dorsal fin-spines.

(i) Pungent spine : Some slight but certainly diagnostic characters serve to distinguish spines of *Synodontis frontosus*, *S. victoriae* and *S. schall*. The small adult size of *S. afro-fischeri* precludes its comparison with the other species.

The spines of *Synodontis victoriae* and *S. frontosus* differ from those of *S. schall* in having a rounded as opposed to a laterally compressed cross-section. The spine of *S. frontosus* may be distinguished from that of *S. victoriae* by its having a low and not a high keel on the anterior face, by its stronger curvature and thirdly, by the longer and more numerous distal serrations on the posterior face.

There are enough complete spines amongst the ninety-six specimens to assign the fossils to *Synodontis frontosus* with reasonable certainty.

(ii) Second dorsal ray : This small, chevron-shaped bone which lies anterior to the pungent spine, is represented by nine almost undamaged specimens.

Vertebrae.

Only six anterior precaudal vertebrae were identified. This paucity of vertebrae is remarkable, especially when compared with the large number of cranial bones preserved. A similarly disproportionate ratio of cranial to axial skeletal parts was noted in the *Clarias* specimens from the same deposit.

It is estimated that the size range of *Synodontis* from this deposit is between 20 and 40 cm standard length; the modal size is about 35 cm.

The minimum number of individuals in the collection (based on the number of frontals preserved) is eighty-six, although the number of dorsal spines indicates a somewhat higher figure.

CYPRINIODEA

Fam. CYPRINIDAE.

Barbus cf. B. bynni and Barbus cf. B. altianalis.

The majority of fish-fossils from Site IX is referable to this genus, which also provides the highest estimated number of individuals.

The fossils consist mainly of branchiocranial elements, particularly lower phararyngeal bones and dissociated pharyngeal teeth; the neurocranium is very poorly represented.

Two fairly clear-cut differences were found in the morphology of the pharyngeal bones and teeth of *Barbus bynni* (FORSK.) and *B. altianalis* (BOULENGER), the species thought most likely to occur in these deposits. On the basis of these characters, I consider that fishes resembling *B. bynni* and *B. altianalis* were present in Lake Edward during the Epi-Pleistocene. Since most of the pharyngeal bones and teeth resemble those of *B. bynni* it seems likely that this was the predominant species, or at least, morphological type (see below).

N e u r o c r a n i u m . — Represented only by the basioccipital, of which there are thirty-four rather fragmentary specimens.

B r a n c h i o c r a n i u m .

H y o m a n d i b u l a . — Ninety specimens (31 left, 59 right) most of which are almost entire and lack only the slender, distal limb.

O p e r c u l u m . — Thirty-three specimens (14 left, 19 right), none entire.

P r e o p e r c u l u m . — Thirty-three fragmentary specimens (17 left, 15 right and 1 indeterminable).

? I n t e r o p e r c u l u m . — A single bone is tentatively identified as an interoperculum.

U r o h y a l . — Two specimens.

C e r a t o h y a l . — Three (2 left, 1 right).

E p i h y a l . — One.

? M e t a p t e r y g o i d . — One almost entire bone has the general appearance of this element.

Q u a d r a t e . — The anterior outline of the articular surface differs slightly in *Barbus bynni* and *B. altianalis*, being almost square in the latter.

On this character, three bones (all left) may be assigned to *Barbus altianalis* and fifty-one (22 left, 29 right) to *B. bynni*. None of these specimens is entire.

A r t i c u l a r . — Thirty-one fragmentary specimens (15 left, 16 right). The point of fracture is remarkably constant, and occurs slightly anterior to the facet.

P a l a t i n e . — Ten almost entire bones (7 left, 3 right).

J a w s .

D e n t a r y . — One hundred and ninety-one specimens (112 left, 79 right). There is some variation in the gross morphology of the fossil dentaries, particularly in the stoutness of the horizontal limb. This variability is, however, within intraspecific limits as determined from the skeletons of present-day fishes. It is impossible to determine the specific identity of the fossils.

M a x i l l a . — Seventy-three specimens (25 left, 48 right) showing various forms of breakage. The maxillae of *Barbus bynni* and *B. altianalis* differ in the nature of the process to which the palato-maxillary ligament is attached. In *B. altianalis* there is a low boss at the point of insertion, whereas in *B. bynni* the ligament is attached to a shelf-like projection. Fossils in which this character can be checked are clearly of the « *bynni* » type.

P r e m a x i l l a . — Two fairly complete specimens (left and right) from fishes of markedly different sizes.

P h a r y n g e a l   b o n e s   a n d   t e e t h .

It is difficult to select trenchant criteria which may be used to separate the pharyngeal bones and teeth of *Barbus bynni* from those of *B. altianalis*. Two characters have been chosen, however, which although showing slight interspecific overlap, prove reliable when large series are available.

One of the characters is the form of the major pharyngeal tooth. The crown of this tooth is globose in *Barbus bynni*, but in *B. altianalis* it is more compressed and mammiform. If the teeth of small specimens are compared, a clearly defined difference is seen in the nature of the cusp. In *B. altianalis* the cusp rises smoothly from the crown, whereas in *B. bynni* it has the appearance of a slight median protuberance from the otherwise convex occlusal surface. It is in the pattern of cusp attrition that the two species show greatest divergence. The low cusp of *B. bynni* is usually worn and only slightly evident even in small individuals; large fishes have the occlusal

surface worn into a definite and extensive pit, so that the originally globose crown becomes distinctly molariform.

Attrition of this type is rarely encountered in *Barbus altianalis*. In this species, wear is slight and restricted to the cusp which retains its mammiform appearance even in large individuals (80 cm standard length).

Such differences in attritional pattern, although modified by the form of the unworn tooth, are probably related to differences in the food of the two species and to the functional relationships of the pharyngeal bones with the horny pad against which they occlude.

The second « specific » character is less readily determined. It is the ratio of the distance between the major pharyngeal tooth and the apex of the angle in the lower limb of the bone, to the length of the lower limb below the apex. In *Barbus bynni* the ventral limb is longer (as much as 1 ½ times) than the distance from apex to major tooth, but in *B. altianalis* it is equal to, or, very slightly shorter than, this distance.

These two characters (used in combination wherever possible) show that most pharyngeal bones and isolated teeth can be assigned to *Barbus bynni*. In fact, only seven bones (3 left, 4 right) are definitely referred to *Barbus altianalis*.

Since they are unit characters, the pharyngeal bones provide a suitable means for estimating the minimum number of fishes represented in the collection. In order to facilitate this calculation the material is divided first, into left and right bones and secondly, into six fracture groups. No group is absolute and there is slight overlap between the various categories.

L e f t   b o n e :

(i) Ventral limb and the major tooth or its « alveolus », with occasionally the succeeding one or two rows of teeth . Tooth present : 93. Tooth absent : 37 (all *Barbus* cf. *B. bynni*).

(ii) The major tooth (or its « alveolus ») together with the bone immediately surrounding it : Tooth present : 37 (*Barbus* cf. *B. bynni*). Tooth absent : 4 (sp. indet).

(iii) The entire or greater part of the dentigerous area; in some specimens either the ventral or dorsal limb is present. Major tooth present : 15. Major tooth absent : 6 (Both groups *Barbus* cf. *B. bynni*). Species indeterminable : 16.

(iv) The dorsal limb and part of the dentigerous surface : 19 specimens, all specifically indeterminable.

(v) Dorsal limb only : 23 specimens, all specifically indeterminable.

(vi) The entire bone : Major tooth present : 11. Major tooth absent :1 (all *Barbus* cf.*B. bynni*). Species indeterminable : 5 (tooth absent, lower limb damaged).

R i g h t   b o n e. — The same breakage groups, as defined above, are used.

(i) Major tooth present : 62. Major tooth absent : 44 (all *Barbus* cf. *B. bynni*). Species indeterminable : 2.

(ii) Tooth present : 37 (*Barbus* cf. *B. bynni*). Tooth absent : 13 (sp. indet.).

(iii) Tooth present : 4 (*Barbus* cf. *B. bynni*). Tooth absent : 8 (sp. indet.).

(iv) Tooth present : 2 (*Barbus* cf. *B. bynni*). Tooth absent : 20 (sp. indet.).

(v) 32 specimens, all specifically indeterminable.

(vi) Tooth present : 6 (*Barbus* cf. *B. bynni*). Tooth absent : 4 (*Barbus* cf. *B. bynni*). Specifically undeterminable : 4.

Barbus altianalis.

L e f t   b o n e. — 4 [three of breakage group (i) and one of group (iii)].

R i g h t   b o n e. — 5 [all of group (ii)], each with the major tooth preserved.

In addition, two isolated major pharyngeal teeth are assigned to *B. altianalis*.

Besides the material described above, there are fourteen small fragments of pharyngeal bones which cannot be identified further.

I s o l a t e d   p h a r y n g e a l   t e e t h :

(i) Major pharyngeal tooth : *Barbus* cf. *B. bynni*. One hundred and sixty-four teeth are referred to this species. The teeth represent a wide size-range of fishes, with the majority derived from large individuals and very few from small fishes. Attrition pattern is variable and apparently without correlation between tooth size and the degree of wear; most teeth show considerable wear and are of the molariform type. In a few specimens almost the entire crown is reduced to a low, flattened surface.

One additional tooth, without pronounced wear, is morphologically intermediate between the major teeth of *Barbus bynni* and *B. altianalis*. It is considered as specifically indeterminable.

Forty-eight fragments are identified as being derived from the major pharyngeal teeth of *Barbus* cf. *B. bynni*.

(ii) Other pharyngeal teeth of *Barbus* sp. or spp. : Sixty-eight teeth; their size-range is similar to that of the major teeth.

As mentioned above, the pharyngeal bones may be used for calculating the minimum number of individuals present in the sample. In this instance the major pharyngeal tooth in association with its bone, or, the alveolus of this tooth, has been used. As many specimens cannot be specifically identified, three estimates of minimal number of individuals must be given : viz. for *Barbus* cf. *B. bynni*; for *B. altianalis*; and for *Barbus* spp.

The estimates are : *Barbus* cf. *B. bynni* 200 fishes; *B. altianalis* 5 fishes; and for *Barbus* spp. 227 fishes.

In the calculations no account was taken of the one hundred and sixty-four isolated major pharyngeal teeth since these could not be assigned to left or right bones. Considering total *Barbus*, it will be seen that the number of bones from either side lacking major teeth is almost equal. (66 left and 81 right). Thus, it would seem reasonable to consider the isolated teeth as being divisible equally into two groups representing those dislodged from left and right bones (the size ranges of isolated teeth and edentulous bones are similar). If one hundred and forty-seven of the teeth are refered to those bones which lack major teeth, then the total minimum number of all *Barbus* is only increased by six individuals.

Axial skeleton.

Vertebrae. — The vertebrae, especially the abdominal elements, of present-day *Barbus bynni* are stouter than those of fishes in the *B. altianalis* sub-species complex. In lateral view, the longitudinal strut of the centrum is seen to be thicker in *B. bynni* than in *B. altianalis* vertebrae. This difference also affects the outline of the centrum when viewed from above : in *B. altianalis* the centrum has a distinct transverse constriction, whereas in *B. bynni* it is only slightly narrowed. Neither of these characters are, however, absolute, particularly when considering large individuals of *B. altianalis*; the validity of their use in the specific identification of this material is doubtful and will be discussed below.

Precaudal vertebrae.

1st Vertebra. — Forty-eight specimens. The centrum shows considerable variation in outline, but in the majority of specimens it is oval, thus differing from the almost circular first vertebra of *Barbus bynni* and *B. altianalis*.

2nd Vertebra. — Fifty-five specimens. Most of the fossils approach the form of the second vertebra in *Barbus bynni* rather more closely than that of *B. altianalis*. In many specimens the centrum is obliquely broken along a dorso-ventral line. This type of fracture is very similar to that resulting from a knife-cut into and through the centrum; it has not been observed in skeletons found in Nature and cannot easily be replicated by manual pressure alone. Judging from the nature of the exposed surface, the damage occurred before fossilization.

Other precaudal vertebrae. — Two hundred and thirty-three well-preserved but specifically unidentifiable specimens. There are approximately equal numbers of anterior and posterior elements.

N e u r a l   s p i n e s . — Four isolated neural spines are identified as those of the fourth vertebra.

R i b s . — The highly characteristic third rib is represented by eighteen specimens (10 left, 8 right). In general appearance these ribs are nearer those of *Barbus bynni* than *B. altianalis*. One other specimen is tentatively identified as a third rib.

Nine fragments of pleural ribs (proximal parts) cannot be further identified.

C a u d a l   v e r t e b r a e . — The majority of these specimens is intermediate in form between the caudal vertebrae of extant *Barbus altianalis* and those of *B. bynni*. They are somewhat coarser than the vertebrae of *B. altianalis* but are less compact and stout than those of *B. bynni*; a few specimens are strictly comparable with similar vertebrae of *B. altianalis*.

Thus it appears that the predominant species in this upper Pleistocene population of *Barbus* combined certain osteological characters (notably the pharyngeal bones and teeth) of present-day *B. bynni* with a vertebral form more nearly akin to that of extant *B. altianalis*.

In general, the three hundred and eight caudal vertebrae are well preserved, but most lack neural and haemal spines. With few exceptions, the centrum is intact.

T e r m i n a l   v e r t e b r a e . — Five damaged specimens.

H y p u r a l s . — Five specimens.

Fin skeleton.

F i r s t   i n t e r n e u r a l   p t e r y g i o p h o r e . — Except for its more robust form in *Barbus bynni*, this bone is similar in both *B. altianalis* and *B. bynni*. The forty-two fossils show varied breakage patterns; none is entire.

S e c o n d   i n t e r n e u r a l . — Several characters serve to distinguish the second interneural of *Barbus bynni* from that of *B. altianalis*. The characters most frequently preserved in the fossils are :

(i) The distal articular surface is almost horizontal in *Barbus bynni*, but is curved and inclined forwards in *B. altianalis*; laterally and below these facets there is an elongate and well-defined fossa in *B. bynni*, but in *B. altianalis* this fossa is barely, if at all, perceptible.

(ii) In *Barbus bynni* the posterior face of the bone is clearly concave, with the sides sloping steeply towards the median spine; in *B. altianalis* this face is only weakly concave and gives the appearance of a gently curved surface divided by the spine. Furthermore, in *B. bynni* the lateral bound-

aries of the concavity turn sharply inwards to join a median, posteriorly directed projection from the anterior surface, whereas in *B. altianalis* the boundaries pass almost imperceptibly into a lateral thickening at the base of the posterior projection.

It was found that although the lateral fossa is generally more definite in specimens designated by other characters as *Barbus* cf. *B. bynni*, intermediates between the « *bynni* » and « *altianalis* » types occurred in specimens assigned to *Barbus* cf. *B. bynni* or to *B.* cf. *altianalis*.

Breakage patterns vary, with the majority of specimens representing the distal third or two thirds of the bone.

Ninety-three specimens are identified as second interneural pterygiophores; of these, eighty-four are referred to *Barbus* cf. *B. bynni* and nine to *B.* cf. *altianalis*.

Third interneural. — The more concave posterior face of this element in extant *Barbus bynni* and differences in the shape of the articular surface, permit fairly certain specific identification.

All the fossils are incomplete, the distal third to two-thirds of the bone being most frequently preserved. Of seventeen specimens, sixteen are assigned to *Barbus* cf. *B. bynni* and one to *B.* cf. *altianalis*.

Fourth interneural. — One specimen (specifically indeterminable).

Three fragmentary specimens are tentatively identified as first (f 2) and second interneural pterygiophores.

Interhaemal pterygiophores. — Three fragmentary specimens are identified as second, third and fourth interhaemals.

Pectoral and Pelvic girdles. — Are each represented by a single, fragmentary specimen.

Third (enlarged) dorsal fin-ray. — There are thirty-one fragments (21 left and 10 right halves) mostly from the proximal fifth to third of this spine-like ray. On the basis of their slight curvature and their massiveness, the specimens are referred to *Barbus* cf. *B. bynni*. Two other specimens should probably be identified as fragments of this ray.

Branched dorsal and anal rays. — It seems probable that most of the two hundred and seventy-nine halves of fin rays recovered from this deposit should be referred to *Barbus*.

Size range and number of individuals. — The size range of individuals present in this sample is estimated to be from 25 to 75 cm. standard length, with a distinct mode between 45 and 60 cm.

The probable minimum number of individuals of both species is two hundred and twenty-seven.

PERCOMORPHI

Fam. CENTROPOMIDAE.

Lates cf. L. niloticus.

No well-defined osteological characters have been found which will enable *Lates niloticus* to be distinguished from the species and sub-species of *Lates* occurring in Lakes Rudolf and Albert. The fossil bones are identical with comparable elements from species of this complex and are considered as representing *L. niloticus*.

N e u r o c r a n i u m. — The few neurocranial bones present are identified as follows :

V o m e r. — The dentigerous surface is preserved in all nine specimens, and the posterior ventral limb in seven. There is some variation in the shape of the toothed area. Basically, this surface is cardiform in outline, but in seven specimens the posterior median margin is produced as either a narrow, or, a broad tongue. Two other specimens have the posterior margin smoothly convex. Some intraspecific variability in this character was observed amongst the extant species and sub-species examined; in these, the posterior outline is usually either somewhat concave or convex. Since so few fossils are available and because this character is known to be inconstant in living fishes, it must be considered of little taxonomic importance. (See also WHITE, 1927).

P a r a s p h e n o i d. — Represented by six fragments, one of which is almost entire; the remainder are from the middle third of the bone.

B a s i o c c i p i t a l. — In all fourteen specimens fracturing has occurred along almost identical lines. The facet and lateral walls immediately anterior to it are preserved, but, as the break runs obliquely ventrad, the anterior part of the bone is represented only by its ventral and ventro-lateral walls.

E x o c c i p i t a l. — Three, fairly complete specimens.

S u p r a o c c i p i t a l. — Three fragments, two from the middle third of the bone and one in which the anterior two thirds are preserved.

B r a n c h i o c r a n i u m.

P a l a t i n e. — Two imperfect specimens (left and right) from fishes of manifestly different sizes.

4

H y p o h y a l. — A single specimen, wanting the dorsal third.

C e r a t o h y a l. — Five specimens (4 left, 1 right), all more or less entire.

H y o m a n d i b u l a. — Three imperfect specimens (1 left, 2 right).

Q u a d r a t e. — Sixty specimens (31 left, 29 right) exhibiting various degrees of completeness, from virtually entire to some in which only the articular surface and ventral limb are present.

A r t i c u l a r. — Thirty-six specimens (13 left, 23 right) of which only two are almost entire. With few exceptions, the remainder show a rather constant fracture point anterior to the facet; in some, breakage has occurred immediately anterior to the facet.

D e n t a r y. — Seventy-two specimens (6 left, 66 right), none entire. The line of fracture is remarkably constant, occurring most frequently somewhat anterior to the point at which the dentary forks into ascending and horizontal rami.

P r e m a x i l l a. — Twenty-three (12 left, 11 right); breakage is varied and only two bones are entire.

M a x i l l a. — Twenty-five specimens (9 left, 16 right), none entire; most specimens are derived from the anterior and antero-lateral portions of the bone.

P r e o p e r c u l u m. — Twenty fragmentary specimens (11 left, 9 right), mostly derived from the region between the ascending and horizontal limbs, although the ascending limb is present, albeit incomplete, in five specimens.

B r a n c h i o s t e g a l   r a y s. — Two specimens, one about two-thirds complete and the other about one-third complete.

G i l l - r a k e r s. — Five well-preserved specimens, all from the first gill-arch (four from the epibranchial and one from the epi-ceratobranchial angle).

F i n   s k e l e t o n.

P e c t o r a l   g i r d l e.   P o s t - t e m p o r a l. — Six fragmentary specimens.

C l e i t h r u m. — Seventeen specimens (6 left, 11 right), all incomplete; the majority is from the region between the ascending and horizontal limbs, but short lengths of both limbs are usually present.

S c a p u l a. — Two incomplete specimens from the ventrolateral portion of this bone, including the trochlea facet.

P e l v i c   g i r d l e. — Five fragmentary specimens (4 left, 1 right) of the posterior transverse face and part of the median longitudinal limb.

Interneural pterygiophores.

First interneural. — Two incomplete specimens.

Third interneural. — This very characteristic pterygiophore is represented by twenty, variously fragmented specimens.

Fourth interneural. — Two incomplete specimens.

One fragmentary and serially indeterminable interneural is tentatively referred to *Lates*.

Interhaemal pterygiophores.

First interhaemal. — Twenty-six well-preserved specimens. A badly damaged fragment, probably from the distal third of this interhaemal, is provisionally referred to *Lates*.

Dorsal and anal fin-spines. — Forty-two spines are tentatively identified as those of *Lates*, although the possibility that some were derived from large individuals of *Tilapia* cannot be overruled. In addition there are two anal spines and two rays which were preserved in their serial arrangement, but which were dislodged during cleaning and development.

Pectoral spines. — Thirty-three (25 left, 8 right) spines may be referred to *Lates*.

Vertebrae.

In general, the vertebrae are well-preserved, although most have their neural and haemal arches broken or missing entirely. There is no indication of rolling or weathering and the finest details of sculpturing and pattern are preserved.

Precaudal vertebrae. — 1st : eleven specimens; 2nd : seven specimens; 3rd : twenty-three specimens; 4th : nine specimens.

Excepting the twelfth vertebra, which is easily recognised by the transverse strut connecting the parapophyses, none of the more posterior precaudal vertebrae was individually identified. There are sixty-three such elements and three twelfth vertebrae.

Caudal vertebrae. — Sixty-one specimens.
Thirty-one fragmentary vertebrae are readily identifiable as those of *Lates*, but they cannot be serially placed.

Ribs. — One specimen, the head of an anterior abdominal rib.

Size range and number of individuals.

From the vertebrae and certain syncranial bones, the size range of individuals represented in this sample is estimated to be from 30-100 cm

standard length, with distinct modes at *ca.* 40 and *ca.* 65 cm. Thus, it is obvious that *Lates* from this deposit were considerably smaller than those from Kaiso beds and beds of the Semliki series in the Lake Edward area.

The estimated minimum number of individuals represented is sixty-six (derived from the dentary).

Fam. CICHLIDAE.

Tilapia sp. indet.

The *Tilapia* remains are interesting because of the disproportionately high number of first interhaemal pterygiophores preserved. Reasons for this disparity may possibly be associated with human activity; it is difficult to imagine any natural sorting process which could produce similar results, particularly since the phenomenon is apparently restricted to one species.

The specific determination of the *Tilapia* fossils has proved impossible.

Branchiocranium.

Hyomandibula. — Four incomplete specimens (all left).

Quadrate. — Three fragmentary and similarly fractured specimens.

Articular. — Ten specimens (5 left, 5 right), of which five are almost entire.

Dentary. — Two incomplete specimens.

Premaxilla. — Six incomplete bones (5 left, 1 right) comprising the anterior third of the horizontal ramus and the major part of the ascending process. It is clear from the alveolar surface that at least five inner series of teeth were present.

Urohyal. — One, almost entire specimen.

Operculum. — Thirty-eight fragmentary specimens (17 left, 21 right).

Suboperculum. — One fairly complete bone.

Fin skeleton.

Post-temporal. — One, almost entire bone.

Pelvic girdle. — Characters serving to distinguish the pelvic girdle of *Lates* and *Tilapia* are neither numerous nor well represented in the fossils; thus, some fragments thought to be from *Tilapia* may be derived from the girdles of small *Lates*.

Ten specimens (4 left, 6 right) are tentatively referred to *Tilapia*; all are very fragmentary.

First interhaemal pterygiophore. — The first interhaemal is the predominant *Tilapia* fossil, being represented by one hundred and ninety-three specimens. Of these, seventeen are virtually entire, with only the attenuated proximal spine broken near its tip; thirty-nine others have at least two-thirds of the bone preserved. The remaining specimens are more fragmentary, but include one in which the first anal spine is still articulated by its delicate double-ring joint. Only a few other bones have the pterygiophore joint intact.

It is impossible to divide this material into well-defined breakage groups since inter-grading fracture types are common.

Fin-spines.

Dorsal fin. — On the basis of their curvature and the inclination of the proximal face, one hundred and forty-seven spines are assigned to *Tilapia*. The material is variously broken and only a few spines are entire; the majority is of the proximal half or less.

Anal fin. — Fifty-one specimens, comprising eighteen first and thirty-three second and third spines. Unlike the dorsal spines, many anal spines are entire, or, almost entire.

Pelvic spine. — Thirty-two (10 left, 22 right).

Vertebrae.

Precaudal vertebrae. — 1st : twenty-six specimens; 2nd twenty-three specimens; 3rd : thirteen specimens.

In addition there are one hundred and thirty-nine precaudal vertebrae of indeterminable position in the column.

Caudal vertebrae. — One hundred and sixty-one specimens, all of indeterminable position.

All vertebrae are well preserved and although many are without neural and haemal spines there is a high proportion of specimens with these delicate structures intact.

Size range and number of individuals.

The modal size of these *Tilapia* is estimated at *ca*. 35 cm standard length, and the size range from *ca*. 30-40 cm. The minimum number of individuals (based on the number of first interhaemal pterygiophores) is one hundred and ninety-three.

PALAEOPTERYGII

Fam. POLYPTERIDAE.

Polypterus sp.

The only specimen from this genus is an almost entire abdominal vertebra. *Polypterus* does not occur in the present fauna of Lake Edward and neither was it found in earlier deposits.

Vertebral form in this family is very characteristic and I have no doubt as to the identity of the specimen.

In appearance and mineralization the *Polypterus* vertebra compares very closely with other specimens from this deposit; thus, there seems little reason to doubt the contemporaneity of *Polypterus* with the other species of the N. F. P. R. Since the fish fauna of the period was so typically Nilotic the presence of *Polypterus* is not unexpected. It is, of course, impossible to give a certain specific identification from one vertebra, but it can be said that the bone compares more closely with the corresponding vertebrae of *P. senegalus* than with those of *P. enderlichi* or *P. bichir*.

The paucity of *Polypterus* remains may reflect the relative scarcity of these fishes in the Epi-Pleistocene lake. Certainly, in present-day Lake Albert, *P. senegalus* is not often or easily captured.

GENERICALLY UNIDENTIFIABLE *PERCOMORPHI*.

(i) 2 fragmentary fin-spines (? *Lates* dorsal and anal spines).

(ii) 23 fin-rays and spines, in which only proximal ends are preserved.

(iii) 5 pectoral spines.

GENERICALLY UNIDENTIFIABLE FRAGMENTS.

Q u a d r a t e. — Fourteen.

V e r t e b r a e. — Four hundred and fifty-three fragments.

It seems likely that the greater number of these fragments should be assigned to *Barbus*. Identification cannot, however, be considered sufficiently certain to permit their inclusion with other material referred to this genus.

H y p u r a l e l e m e n t s. — Thirteen.

P t e r y g i o p h o r e s . — Eighty-eight; interneurals of the *Barbus* type predominate.

? B a s i o c c i p i t a l . — Thirteen.

U n i d e n t i f i a b l e   b o n e s . — Ninety-eight, of which seven are den-tigerous.

SITE Xa

Ishango, at the source of the Semliki. Excavation in the post-emersion zone (Z.POST-EM.), trench N 43ᴳ E, between 7 and 23 metres. M e s o-l i t h i c; a kitchen midden.

DIPNOI

Fam. LEPIDOSIRENIDAE.

Protopterus sp.

A large fragment of upper tooth-plate.

OSTARIOPHYSI

SILUROIDEA

Fam. BAGRIDAE.

Bagrus sp.

The presence of *Bagrus* in this deposit is of particular interest. The only other unequivocal record of this genus in the Lake Edward basin is from deposits at Kanyatsi (Lower Kaiso age). The apparent absence of *Bagrus* from the generically rich site IX (N.F.PR.) is enigmatic and remains unexplained.

Neurocranium.

Frontal. — Eight specimens (4 left, 4 right) derived from the posterior part of the bone. All are well preserved, with the finest details of sculpturing intact; breakage is varied.

Supraoccipital. — Two specimens; one almost entire but lacking its posterior spine, the other rather extensively damaged.

Sphenotic. — A single, almost complete bone (left).

Parasphenoid. — Two fragments, from the middle third of the bone and with almost identical fracture lines in both the horizontal and vertical planes.

Basioccipital. — Four specimens, each comprising the facet and posterior third, or, quarter of the bone; the dorso-lateral face is broken in all.

Branchiocranium.

Hyomandibula. — Two specimens (left and right); the left is almost complete but the right comprises only its articular head.

Quadrate. — Two fragmentary specimens.

Articular. — Six specimens (4 right, 2 left).

Dentary. — Fifteen specimens (6 left, 9 right). With three exceptions, only the anterior (symphysial) portion is preserved; in the exceptional bones the greater part of the horizontal limb is present.

In addition, two fragments of dentigerous bone are thought to be derived from the dentary of *Bagrus*.

Vertebrae. — The centrum of the anterior fused vertebral mass is represented by twelve variously fragmented specimens. There is also a fragment from the anterior, median crest of this bone, and four well-preserved specimens of the centrum which lies between the compound vertebra and the basioccipital facet.

Precaudal vertebrae. — Forty-three specimens.

Caudal vertebrae. — Forty-six specimens.

Fin skeleton. — The pectoral girdle is represented by two fragments (left) which include the articular fossa and short portions of the ascending and horizontal limbs immediately adjacent to it. There are also two

fragmentary post-temporals (left and right, but from different individuals) and one incomplete scapulacoracoid.

F i n - s p i n e s .

D o r s a l. — Three specimens (one almost complete and two from the proximal third and quarter). Three fragments from the distal part of the spine are tentatively assigned to this genus.

P e c t o r a l   s p i n e. — Twelve (5 left, 7 right). None is entire, but the complex articular head is well-preserved in all. There is also a fragment which is probably from the distal portion of the spine.

Fam. CLARIIDAE.

Clarias sp.

One fragment of neurocranial roofing bone (possibly the post-frontal) and four vertebrae (3 precaudal and 1 caudal, from at least two individuals) are the sole remains of *Clarias* in this collection. A fragment of parasphenoid may be derived from a *Clarias*.

CYPRINOIDEA

Fam. CYPRINIDAE.

Barbus sp. (probably B. bynni).

D e n t a r y. — Two rami (left and right) from different fishes.

A r t i c u l a r. — One rather fragmentary specimen (left).

P h a r y n g e a l   b o n e s   a n d   t e e t h. — Two incomplete right bones, comprising the lower limb, major pharyngeal tooth and part of the dentigerous area. In addition there is the crown of a very large major pharyngeal tooth whose gross morphology is similar to that of the unworn tooth in *B. bynni*.

V e r t e b r a e. — Nine precaudal and twenty-one caudal elements.

Apart from the large pharyngeal tooth, apparently only two fishes (with estimated standard lengths of 30 and 50 cm) are represented by this material.

PERCOMORPHI

Fam. CICHLIDAE.

Tilapia sp.

Tilapia are poorly represented by the following fragments :

A r t i c u l a r. — One, almost complete specimen.

V e r t e b r a e. — Two precaudal (possibly second vertebra) and eleven caudal vertebrae.

F i n - s p i n e s.

P e c t o r a l. — One almost complete right spine. The proximal two-thirds of another spine, lacking the diagnostic articular head, is tentatively identified as *Tilapia.*

D o r s a l f i n. — Twenty spines (about equal numbers of anterior and posterior spines) are tentatively referred to this genus.

A n a l f i n. — Two spines.

S i z e r a n g e. — These few specimens were derived from fishes between *ca*. 35 and 45 cm standard length.

GENERICALLY UNIDENTIFIABLE MATERIAL.

V e r t e b r a e a n d f r a g m e n t s o f v e r t e b r a e. — Twenty-one.

F i n - r a y s a n d s p i n e s. — Two.

U n i d e n t i f i a b l e f r a g m e n t s. — Two.

Fam. CENTROPOMIDAE.

Lates sp.

V e r t e b r a e. — Two abdominal and one caudal vertebrae. The abdominal elements have the same appearance as other specimens from this deposit, whereas the caudal vertebra is lighter in colour and has an adherent matrix similar to that of fossils from the N.F.PR.

D e n t a r y. — The anterior two thirds, from a small fish. The specimen is relatively well-mineralized.

SITE X*b*

As for Xa, but trench N 143ᴳ E, between 15 and 19 metres.

OSTARIOPHYSI

SILUROIDEA

Fam. BAGRIDAE.

Bagrus sp.

Dentary. — Two specimens (left and right rami, from different individuals) in which only the dentigerous surface is preserved.

Pectoral girdle.

Cleithrum. — Two fragmentary specimens, one of the ventral margin of the ascending limb, the other from the median aspect of the cleithrum near its point of union with the mesocoracoid.

Pectoral fin-spines. — Two almost entire spines (left and right). Slight size differences suggest that they are from different individuals.

Vertebrae.

Anterior fused vertebral mass. — Three specimens, all derived from the antero-ventral aspect of this structure, together with three specimens of the vertebra which lies between the compound vertebra and the skull.

Precaudal vertebrae. — Thirteen.

Caudal vertebrae. — Twenty-seven.

The estimated size range of the fishes represented by these bones is *ca.* 45-80 cm standard length, with a mode at *ca.* 65 cm.

Fam. MOCHOCIDAE.

Synodontis cf. S. frontosus.

Frontal. — Two incomplete fragments (left and right) probably from different individuals. The ornamentation is nearest that of *Synodontis frontosus*.

In addition, there is a small and unidentifiable fragment of neurocranium.

Pectoral fin-spines. — Six specimens (4 left, 2 right) from the proximal end, and two from the distal end of the spine.

Fam. CLARIIDAE.

Clarias cf. C. lazera and probobly also C. mossambicus.

The species are identified on the basis of neurocranial ornamentation; those specimens tentatively referred to *Clarias mossambicus* are clearly in the minority.

Neurocranium.

Dermethmoid. — Ten (five from the anterior portion, including the lateral horn, and five from the posterior quarter to half). The indentation between the horns is more acute than that observed in living *Clarias lazera* and *C. mossambicus*.

Prefrontal. — Two, both incomplete.

Pterotic. — Two large fragments, one right, the other probably left.

Frontal. — Five small fragments.

Supraorbital. — Two fragments.

Post-temporal. — Two (left and right, from different fishes), both incomplete.

Unidentifiable neurocranial fragments. — Twenty-six, of which three may be tentatively assigned to *Clarias mossambicus*.

Hyoid arch.

Ceratohyal : one (right); epihyal : two (both right) and one fragment (left).

Quadrate. — One; almost entire.

Articular. — Eight almost perfect specimens (6 left, 2 right).

Pectoral fin-spines. — Four specimens from the proximal part of the spine, and three from the middle section.

Vertebrae. — Twelve precaudal and twelve caudal elements.

Size range. — The size-range of individuals represented by these bones is estimated at between 55 and 75 cm standard length, with a mode at *ca.* 60 cm.

CYPRINOIDEA

Fam. CYPRINIDAE.

Barbus sp.

Barbus is represented only by five vertebrae (2 precaudal and 3 caudal) from fishes of *ca.* 30 and 35 cm standard length.

PERCOMORPHI

Fam. CICHLIDAE.

Tilapia sp.

Vertebrae.

Precaudal. — Thirty-seven, of which nine are identified as first vertebrae.

Caudal. — Nineteen specimens.

Interneural pterygiophores.

Two first interneurals; cne almost complete, the other comprising the articular surface only.

Fin-spines.

One pectoral spine and fifteen dorsal spines. The latter can only be tentatively identified as *Tilapia*, since few characters are preserved which will enable them to be differentiated from similar spines of small *Lates*.

The estimated size range of the fishes represented by this material is from 30-45 cm standard length.

Fam. **CENTROPOMIDAE.**

Lates sp.

V e r t e b r a e . — Two specimens, one of which is poorly preserved and has an adherent matrix unlike that of other specimens from this level. The second specimen (an abdominal element) is markedly well-mineralized and appears to be somewhat rolled. It seems very probably that both specimens were derived from older deposits.

GENERICALLY UNIDENTIFIABLE MATERIAL.

(i) A fragment of siluroid pectoral spine.

(ii) Four fragments from the proximal ends of soft fin-rays.

(iii) A small fragment of parasphenoid.

(iv) Fourteen vertebrae.

SITE X*c*

As for site Xa and b, but trench N 43ᴳ E, between 0-9 metres.

OSTARIOPHYSI

SILUROIDEA

Fam. **BAGRIDAE.**

Bagrus sp.

N e u r o c r a n i u m.

S u p r a o c c i p i t a l. — Four specimens, variously fragmented and none entire.

S p h e n o t i c. — One almost entire (right).

F r o n t a l. — One small fragment.

B a s i o c c i p i t a l. — Five specimens, all virtually entire.

Branchiocranium.

Quadrate. — One; fragmentary.

Articular. — One; almost entire.

Epihyal. — One; slightly damaged.

Ceratohyal. — Three specimens (1 left, 2 right), all incomplete, together with a small fragment which includes the epi-ceratohyal suture.

Hypohyal. — Three specimens (right); two of these are almost entire and one is a fragment from the postero-dorsal margin.

Dentary. — Nine (3 left, 6 right); none entire.

Vertebrae.

Anterior fused vertebral mass. — Sixteen specimens; none entire. The centrum of this compound vertebra is the only portion represented, except for a fragment from the anterior aspect of the flanged and curved « neural spine ».
Five specimens are identified as the small, flattened first vertebra.

Precaudal vertebrae. — Fifty specimens; the majority being of the first three vertebrae.

Caudal vertebrae. — Forty-two specimens.

Pectoral girdle.

Post-temporal. — Five specimens, four of which are rather fragmentary and one almost entire.

Cleithrum. — Eight fragments, of which six are derived from the area including and surrounding the articular fossa for the pectoral spine.

Coracoid. — Almost the entire posterior part; including the articular surfaces.

Fin-spines.

Pectoral spines. — Seven incomplete spines (2 left, 5 right) together with a fragment from the head of an eighth specimen.

Dorsal spine. — Four specimens from the proximal part of the dorsal spine, and a fifth fragment from the middle section.

Size range. — The estimated size-range of the fishes represented by these various bones is 30-70 cm standard length; most individuals are in the 60-70 cm class.

Fam. CLARIIDAE.

Clarias cf. C. lazera and Clarias cf. C. mossambicus.

As with specimens from other deposits, the specific identification of this material is based on the ornamentation of neurocranial bones. Again, *Clarias mossambicus* is poorly represented.

Neurocranium.

Dermethmoid. — Six variously fragmented specimens, of which three are almost entire.

Prefrontal. — Four incomplete bones (2 left, 2 right) and probably a small fragment of prefrontal.

Supraorbital. — One specimen, from the anterior part of the bone.

Frontal. — Thirteen fragments (5 left, 7 right and one indeterminable), ten of which are derived from the area including, or, immediately surrounding the fontanelle, and three are from the anterolaterally expanded portion of the bone. Wherever the post-fontanelle sutural surfaces are preserved, they are, with one exception, of the *Clarias lazera* type (see p. 34), as is the surface ornamentation. The exceptional specimen compares closely with *C. mossambicus* in both these characters.

Supraoccipital. — Five; all incomplete.

Post-temporal. — Five, rather fragmentary specimens, of which two are definitely and three are tentatively identified as post-temporals.

Unidentifiable fragments of neurocranium. — Twenty-two.

Branchiocranium.

Palatine. — Two; one entire the other slightly damaged.

Epihyal. — Two (left and right); almost complete.

Urohyal. — One specimen.

Articular. — Three (2 left, 1 right); all well-preserved.

Dentary. — One specimen, lacking the posterior part.

Vertebrae. — Seven posterior precaudal vertebrae.

Fin girdles.

Pectoral girdle. — Represented by : (i) an almost complete right cleithrum; (ii) a fragment of left cleithrum; (iii) a small fragment from the clavicle.

Fin-spines.

Pectoral spines. — Six spines (4 left, 2 right) showing various lines of fracture. In none is the articular head without some slight damage.

Size range.

The estimated size-range of fishes represented by this sample is from 40-75 cm standard length.

Fam. MOCHOCIDAE.

Synodontis sp.

No characters permitting specific differentiation are preserved in this material, which comprises :

(i) An almost entire dorsal fin-spine.

(ii) Two pectoral spines (left and right) and a fragment of pectoral spine.

GENERICALLY UNIDENTIFIABLE SILUROID REMAINS.

Seven fin-spine fragments.

CYPRINOIDEA

Fam. CYPRINIDAE.

Barbus sp.

Vertebrae. — Five caudal vertebrae.

Weberian ossicles. — One fragmentary tripus.

PERCOMORPHI

Fam. CENTROPOMIDAE.

Lates sp.

Only three bones, a caudal vertebra from a fish *ca.* 72 cm standard length and a fragment of dentary, together with a pectoral spine (also from a small fish), can be referred to this genus. Although the identity of the fin-spine might be called to doubt, there can be no confusion regarding the vertebra and dentary.

The vertebra and fin-spine are heavily mineralized and differ markedly from other specimens in this deposit; they were, thus, probably derived from earlier strata. The dentary, on the other hand, is poorly mineralized and its state of preservation is strictly comparable with the other specimens from this site.

Fam. CICHLIDAE.

Tilapia sp.

V e r t e b r a e. — Seven anterior precaudal vertebrae. Six of these are derived from a fish, or fishes about 45 cm standard length, and the seventh from a slightly larger individual.

F i n - s p i n e s.

D o r s a l   f i n. — Fifteen spines, all from fishes of a size comparable with those from which the vertebrae were derived. Two of the spines are lighter in colour and less mineralized than the others.

A n a l   s p i n e. — One.

P e c t o r a l   s p i n e. — One specimen, complete except for its most distal extremity.

GENERICALLY INDETERMINABLE MATERIAL.

(i) Parasphenoid (middle section).
(ii) Fragment of basioccipital.
(iii) Two articulars (from different genera).
(iv) Two halves of soft fin-rays.
(v) Twelve vertebrae.
(vi) One hypural element.
(vii) Sixteen unidentifiable fragments.

DISCUSSION AND SUMMARY.

Before considering the evidence furnished by the fossils described in this paper, some attention must be given to the faunal affinities of the fishes inhabiting present-day Lake Edward.

When attempting to discover this relationship, the cichlid and non-cichlid elements should be examined separately. Of the twenty-four non-cichlid species recorded, only three are endemic to Lake Edward. Seven species have a relatively restricted geographical distribution within the area surrounding the lake, although three of these species also occur in Lake Kivu, and the range of one of these extends to Lake Tanganyika. One species otherwise only occurs in Lakes Kivu and Victoria, another is known only from Lake Victoria, a third occurs in Lakes Victoria and Nyasa; and finally, there is one species which, apart from its being recorded in Lake Edward, is known only from the streams of Mount Kilimanjaro.

The remaining ten species may be considered as Nilotic, with some species widely distributed in East Africa. It is interesting to note that five of the ten Nilotic species do not occur in Lake Victoria. A point of probable significance is that the three endemic species and the six species with restricted distribution are all small cyprinids and cyprinodonts, whereas the Nilotic species are mostly large fishes.

The *Cichlidae* show dual affinity. The *Tilapia* species are Nilotic but the *Haplochromis* are clearly related to species endemic to Lake Victoria; three *Haplochromis* species and one monotypic genus are common to both lakes. (Data derived from POLL, 1939; POLL and DAMAS, 1939; TREWAVAS, 1933).

Perhaps the most outstanding feature of the Lake Edward ichthyofauna is the absence of several families which are widespread in eastern and tropical Africa; the *Polypteridae*, *Characidae*, *Citharinidae*, *Schilbeidae*, *Mochocidae*, *Malapteruridae*, *Centropomidae* and *Mastacembelidae* are all without representatives. Furthermore, as compared with Lakes Albert and Victoria, there are fewer genera per family in Lake Edward. In certain respects this absence of otherwise widely distributed families is paralleled in Lake Victoria, although here only the *Polypteridae*, *Citharinidae*, *Malapteruridae* and *Centropomidae* are absent.

DE HEINZELIN (1955) has aptly described the contemporary fauna of Lake Edward as « ... une faune pauvre, tronquée, dépourvue de bon nombre d'éléments qu'on s'attendrait à y trouver... ».

Data summarised in Table I show that during the Pleistocene, gradual changes took place in at least the generic constitution of the fish-fauna of the Edward basin. It is also obvious that until Makalian times (Epi-

The earliest fish-fossils in the Edward basin are from deposits of Kaiso-age. DE HEINZELIN subdivides these deposits into four series on the basis of the Mollusca present. Following his classification, the fishes found at Kanyatsi (Sites I and II) are from Series I, which was laid down in a period of relative aridity, tentatively correlated with WAYLAND's « Kageran Interpluvial ».

The only other fish-bearing Kaiso deposits which can be refered to one of DE HEINZELIN's sub-divisions are those from Sites IV, V and V a. These are placed in series III which post-date the Kageran interpluvial; at the time of their deposition the climate was relatively humid (DE HEINZELIN, op. cit.). This assemblage contains typically Nilotic genera and does not differ from the generic complex preserved at Kanyatsi (Kaiso Series I).

Thus, the fish-fossils provide little evidence on the effect and intensity of the first (Kageran-Kamasian) interpluvial arid period. It is clear from the fossil Mollusca, however, that there was a gradual increase in the concentration of dissolved salts during the period prior to their preservation. The increased salinity had the effect of producing a gastropod fauna with a pseudomarine facies (DE HEINZELIN, op. cit.; FUCHS, 1936; BEAUCHAMP, 1946).

WORTHINGTON (1932; 1937) and WAYLAND (1934) (whose opinions were based on those of WORTHINGTON), considered the first interpluvial to be of such aridity as to almost completely dry out the lake. It is to this period that WORTHINGTON (1932; 1937), using the palaeontological data then available, ascribed the major change in the affinities of the Lake Edward fishes. But, as mentioned above (p. 67), such an early date for this event can no longer be entertained. Evidence from Series III Kaiso fossil shows clearly that after the Kageran-Kamasian interpluvial Lake Edward was still populated by fishes of a Nilotic type, including many of the present-day absentee genera.

There are two possible explanation for this phenomenon. One explanation would assume that the Kageran fish-fauna was destroyed during the interpluvial, but, with the increased rainfall of the second (Kamasian) Pluvial, Lakes Edward and Albert were once again connected; this hypothesis also assumes that Lake Albert was little affected by the inter-pluvial arid period and that fishes from the lake would be able to recolonize Lake Edward. The second explanation assumes that aridity in the Edward basin was insufficient to destroy the Kageran fish-fauna, which persisted; this theory has, of course, the necessary correlate that the majority of fishes was not adversely affected by the increased salinity of the water (see above).

From the data available it is difficult to decide which hypothesis can be considered the more reasonable, but, recent research seems to provide less support for the concept of an intensely arid interpluvial. As mentioned earlier, fish-fossils from certain Lake Edward Kaiso-beds were interpreted to show almost complete desiccation of the lake because they apparently represented the last record of certain Nilotic species in the Edward basin.

The earliest fish-fossils in the Edward basin are from deposits of Kaiso-age. DE HEINZELIN subdivides these deposits into four series on the basis of the Mollusca present. Following his classification, the fishes found at Kanyatsi (Sites I and II) are from Series I, which was laid down in a period of relative aridity, tentatively correlated with WAYLAND's « Kageran Interpluvial ».

The only other fish-bearing Kaiso deposits which can be refered to one of DE HEINZELIN's sub-divisions are those from Sites IV, V and V a. These are placed in series III which post-date the Kageran interpluvial; at the time of their deposition the climate was relatively humid (DE HEINZELIN, op. cit.). This assemblage contains typically Nilotic genera and does not differ from the generic complex preserved at Kanyatsi (Kaiso Series I).

Thus, the fish-fossils provide little evidence on the effect and intensity of the first (Kageran-Kamasian) interpluvial arid period. It is clear from the fossil Mollusca, however, that there was a gradual increase in the concentration of dissolved salts during the period prior to their preservation. The increased salinity had the effect of producing a gastropod fauna with a pseudomarine facies (DE HEINZELIN, op. cit.; FUCHS, 1936; BEAUCHAMP, 1946).

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This view is no longer tenable in its original form; furthermore, on DE HEINZELIN's dating these fishes were from post-interpluvial deposits. In Lake Albert, WAYLAND (1926) considered that the Kaiso bone-beds were indicative of a period of intense aridity during which the lake almost dried up. From their associated molluscan fauna, however, both these sites should be equated with DE HEINZELIN's Series III and IV (post-Kageran interpluvial) when, in the Edward basin, the climate was humid.

SOLOMON (1939) does not agree with WAYLAND's climatic deductions from the Lake Albert Kaiso-beds. On the contrary, he considers their ferruginous, sandy, fossiliferous horizons to be indicative of either « ... slightly more open water conditions... » (than the preceeding clays which were laid down under swamp conditions), or « of more complete desiccation than postulated by WAYLAND ». SOLOMON favours the interpretation of more open-water conditions. His reasons for this are that the fossils comprise mainly fishes, crocodiles and hippopotami, and that other mammalian remains are never found as complete skeletons, which would be the case if the animals had died around gradually diminishing water-pools, as suggested by WAYLAND. Instead, the mammalian remains are found as individual bones apparently washed into position. SOLOMON's conclusion is of interest since it parallels DE HEINZELIN's opinion that the climate during the later Kaiso period was relatively humid.

There remain, then, only the Kanyatsi deposits (Kaiso Series 1) as evidence for a period of aridity. Again, the fishes provide little satisfactory information regarding the intensity and effects of this dry phase. Only one genus, *Hydrocyon*, does not reappear in deposits younger than the third Kaiso level. The associated gastropod Mollusca, on the other hand, seem to indicate an increase or change in the salinity of the water, in response to which there evolved a number of spinous and carinate species (DE HEINZELIN, *op. cit.*; FUCHS, 1936). Most of these species do not occur in later Kaiso beds. Their virtual disappearance has been taken to indicate that they were destroyed by the lake drying up (FUCHS, *op. cit.*; BROOKS, 1950). Yet, an alternative and opposite explanation seems feasible. If it is accepted that the spinous and carinate facies was a response to increased salinity, is it not possible that the morphological type might be changed when the water was freshened during subsequent periods of increased rainfall ? Or, alternatively, the species may have been unable to adapt themselves to the new « freshwater » conditions and were destroyed, not by aridity, but by increased humidity.

On the evidence available, it only seems possible to say that during the Kageran-Kamasian interpluvial the lake underwent an increase, or change, in salinity caused by a period of relative aridity. At present the intensity of this arid period cannot be accurately determined.

Fishes from the Middle Pleistocene (Kamasian period, *sensu lato*) are very poorly represented by specimens from one deposit at Katanda amont (Sites VI and VII) in the upper Semliki Valley. DE HEINZELIN places these

deposits in the Semliki-Series of the Middle Pleistocene. The fish-fossils require little comment, except to note that the genus *Barbus* makes its first appearance. There are too few fossils from these beds to give any indication of faunal relationship, but two typically Nilotic genera, *Synodontis* and *Clarotes*, were probably present.

The Middle Pleistocene was an important period in the evolution of the fish-fauna of Lake Edward. All evidence points towards this period as the time when the lake probably received its major influx of fishes from Lake Victoria. The result of this invasion is most clearly seen in the Lake Edward species flock of the cichlid genus *Haplochromis*. The *Haplochromis* species of Lake Edward and Victoria are more closely related to oneanother than to any other *Haplochromis* flock in Africa. There can be no doubt that the two flocks were derived from the same ancestral species group, which had probably reached an advanced stage of adaptative divergence when the flocks were separated. Not only are the majority of species very similar, but three species of *Haplochromis* and one related monotypic genus occur in both Lake Edward and Lake Victoria.

Another important evolutionary factor associated with the Middle Pleistocene was the loss of direct contact between Lakes Edward and Albert (DE HEINZELIN, *op. cit.*, and *in litt.*). From this time onwards Lake Edward must be considered as a discrete faunal unit.

Arguing from evidence supplied by fishes preserved in the Epi-Pleistocene, Ishango beds, it is apparent that the postulated climatic oscillations of the Upper Pleistocene had few long-term effects on the nature, or, affinities of the fish-fauna. This evidence derives from the still typically Nilotic facies of the Epi-Pleistocene and even early Holocene fishes, which could well be described as a segment of the modern Lake Albert fauna. This relationship between the Epi-Pleistocene fauna of Lake Edward and that of modern Lake Albert includes not only the genera *Lates* and *Synodontis*, but also extends to the species level in these and other genera (see Table I and pages 29-54).

The conclusion that there was continuity of faunal type in Lake Edward is, however, dependant upon the assumption that contact between this lake and Lake Albert was lost and not re-established after the Middle Pleistocene. If this can be accepted, and there is little evidence to the contrary, then the typically Nilotic mid-Pleistocene fishes must have persisted in the Edward basin despite postulated extremes of climate (see WAYLAND, 1934, and WORTHINGTON, 1937). It seems most improbable that *Lates*, a species with low tolerance to deoxygenated waters (FISH, 1956) could have survived if the lake was reduced to swamp conditions.

Furthermore, if it can be accepted that the major invasion of fishes from Lake Victoria took place during the Middle Pleistocene, then the extant *Haplochromis* would indicate that the lake did not suffer severe desiccation during the Upper Pleistocene.

DE HEINZELIN (*op. cit.*), summarizing data relating to climatic changes detectable in Pleistocene deposits of the Lake Edward basin, finds no traces of the postulated three intra-pluvial maxima during the Gamblian, but only for an important wet phase corresponding to the Gamblian *sensu lato*. He does, however, find indications of a probable arid phase prior to the Makalian pluvial. The fishes apparently survived this dry phase. If, at this time, the lake basin had achieved its present form, the deeper parts may well have provided a refuge for many species.

Because there are so few Middle Pleistocene fish-fossils, it is impossible to assess the significance of species which, although present in Kaiso and Epi-Pleistocene deposits, are not recorded from the intervening Middle Pleistocene beds. Two genera, *Protopterus* and *Bagrus*, which occured in Kaiso deposits are not represented amongst the mid-Pleistocene material. *Protopterus* is recorded from Epi-Pleistocene beds, but *Bagrus* does nor reappear until it becomes the predominant fish-fossil of the latest deposits of Z.POST-EM., which are typically Mesolithic and of Holocene age.

The Epi-Pleistocene fishes are especially well-preserved and in most genera it is possible to identify the species present.

Both species of large *Clarias* (*C. lazera* and *C. mossambicus*) at present inhabiting Lake Edward are represented as fossils. Also, a few skull fragments have been tentatively identified as *Heterobranchus*, a clariid genus, once thought to be absent from the Edward basin, but recently discovered in the lake (HULOT, 1956).

Two *Barbus* species, *Barbus* cf. *B. bynni* and *Barbus* cf. *B. altianalis* are recorded. Although only *Barbus altianalis* survived until the present-day, the greater number of specifically identifiable fossils is nearer the Nilotic *B. bynni* (see p. 42).

In a preliminary list of the Ishango fishes (published in DE HEINZELIN, 1955) two species of *Synodontis*, *S. nigrita* and *S. schall*, were given. Further study of the fossils showed, however, that the specimens previously identified as *S. nigrita* should be referred to *S. frontosus*.

Specimens of *Lates* from the N.F.PR. Ishango deposits are provisionally refered to *L. niloticus* since no clear-cut differences are manifest in the skeletons of the various species or sub-species in the extant *L. niloticus* complex.

No specific identity can be given to the *Tilapia* remains, which are peculiar in that the majority of specimens is of the first anal pterygiophore; other skeletal parts are less well represented, especially in comparison with other species. No immediate explanation can be provided for this biased sample of *Tilapia.*

The Ishango fishes do not yield any information on the ecological conditions obtaining at the time of their preservation. Furthermore, since the N.F.PR. (Epi-Pleistocene) deposit is probably a sub-aquatic kitchen-midden and the Z.POST-EM. (Holocene) deposit a subaerial kitchen-midden, the

assemblage of species may be artificial; that is, either representative of species which were caught by man, or, of species which were attracted to the area by domestic refuse thrown into the water.

Before considering the critical phase during which the Edward fish-fauna underwent alterations leading to its present truncated and impoverished form, it is necessary to examine the fishes preserved in the most recent deposit (Site X), which is Mesolithic and of Holocene age. Unfortunately, most of these specimens can only be identified as far as the genus. But, amongst the genera preserved are *Lates* and *Synodontis*, two Nilotic genera which have since become extinct in the area. The other genera occur in present-day Lake Edward. The *Lates* specimens are more heavily mineralized than are the other specimens from this deposit and may therefore be derived from an earlier (Epi-Pleistocene ?) deposit. The *Synodontis* remains, on the other hand, are only lightly mineralized and compare closely with the other fish remains from the Holocene beds. It is therefore difficult to interpret the significance of the specimens. Two explanations seem possible : first, a few populations of *Synodontis* survived the critical phase but were unable to maintain themselves, possibly through changed ecological conditions affecting breeding habits, or, secondly, the fossil bones were derived from fishes caught below the Semliki falls and brought back to the settlement at Ishango. Neither explanation is entirely satisfactory and the question of their provenance should remain open.

Thus, from the fossil fishes alone it is impossible to date the changes which took place in the fundamental relationships of the fish-fauna of Lake Edward. Other evidence of environmental changes occurring in Epi-Pleistocene and early Holocene times (DE HEINZELIN, 1955) suggests, however, that the ichthyofaunal hiatus could have been contemporaneous.

Since the present affinities of Lake Edward fishes are both Nilotic and Victorian, there are two important questions relating to this hiatus : first, what environmental factors can be implicated; and secondly, why did certain Nilotic species survive whilst others were killed off ?

A probable answer to the first question is provided by DE HEINZELIN's opinion that volcanicity, coupled with changes in the chemical composition of the water, was the major factor influencing faunal changes. Indeed, it seems that during this period of intense and local volcanic activity (DE HEINZELIN, 1955), Lake Edward could have undergone hydrological changes leading to conditions comparable with those of present-day Lake Kivu. That is, the lower water-strata would become heavily charged with dissolved toxic substances (hydrogen-sulphide, carbonic acid and ammoniacal salts) and would be azooic at all times. Because Lake Edward is relatively shallow and occupies a basin of different shape to that of Kivu, even the surface waters could be polluted during intervals of water-mixing and overturn. Present-day Lake Edward differs from Kivu where no overturn and mixing of surface and bottom waters occurs.

That Lake Edward did not remain in a Kivu-like condition was probably due to three major factors : a different sub-aquatic topography; the existence of large affluent streams flowing into the lake through country distant from the centres of volcanic activity, and thirdly, hydrographical conditions allowing for periodic mixing of the epi- and hypolimnia, thereby preventing the formation of a permanent, dense lower layer.

If such postulated conditions of foul water did obtain, even for a relatively short period, it is not surprising that many species suffered local extinction. It is, in fact, rather more difficult to understand how so many species survived. Presumably for these species survival was the result either of their temporarily colonizing affluent rivers and the areas adjoining river mouths (where some freshening of the water might be expected), or, of the inherent ability of the species to tolerate the hydrological conditions then existing. A possible factor influencing the decline and ultimate extinction of these species might be the loss of suitable breeding grounds through changes in the ecology of the lake. Consideration of this and other ecological conditions affecting late Pleistocene and early Holocene fishes leads directly to the second question posed above.

Speculation is hampered by the lack of fundamental information on the physiological requirements and breeding habits of many of the species concerned. Some data are available on the respiratory characteristics of *Lates* (FISH, 1956). These suggest that the species is intolerant of reduced oxygen and increased carbon dioxide tensions. It is therefore reasonable to infer that breeding would be unsuccessful (if it occurred at all) under such conditions. Regrettably, nothing is known about the physiology of members of the *Characidae* and *Schilbediae*, or of the majority of *Cichlidae* and *Cyprinidae*. In Lake Edward the latter family provides an intriguing puzzle. Two species of *Barbus* coexisted in Lake Edward during the upper Pleistocene. One species closely resembled the Nilotic *B. bynni*, the other resembled *B. altianalis*, a species occurring in Lakes Edward, Victoria and Kivu. Only *B. altianalis* survived the critical Epi-Pleistocene and early Holocene periods.

Indirect evidence on the physiological adaptability and tolerance of these various families can be derived from Lake Kivu. The fish-fauna of this lake is even poorer than that of Lake Edward, from which source it was derived (POLL, 1939), probably at some time after the invasion of Edward by certain Victoria species. The point of particular significance is that all the absentee families of Lake Edward are also absent from Lake Kivu. Since volcanicity played an important part in the evolution of both lakes (Lake Kivu was formed during the middle, or, late Pleistocene by the Mfumbiro volcanic chain damming the valley of a river flowing into Lake Edward) the conclusion seems inescapable that representatives of these families were unable to surmount the ecological and hydrological conditions associated with volcanicity. The more extreme hydrological conditions of

Lake Kivu may also account for the absence of *Bagridae* and *Mormyridae* from the lake. It is difficult to explain the absence of *Lepidosirenidae*, *Cyprinodontidae* and *Anabantidae* on the grounds of adverse ecological conditions since in other lakes all three families tolerate deoxygenated and stagnant water. But here again, factors connected with breeding may have been ultimately responsible for the local extinction of these families.

In conclusion, the faunal affinities of Lake Edward must be reconsidered, particularly in view of the recent classification proposed by WORTHINGTON (1954). Data from the extensive fossil collections reviewed above show clearly that for a considerable period the fish-fauna of Lake Albert was broadly comparable with that of Lake Albert. The correspondence is not exact, because certain Albertine genera apparently never populated the Edward basin. The evolution of the present Edward fauna has been brought about by two principal factors : first, the effects of extreme environmental conditions which further reduced the number of Albertine species, and secondly, the invasion of Lake Edward by certain species of fishes from Lake Victoria. Although the results of this invasion are impressive, they are virtually restricted to one genus, *Haplochromis*, and must not be allowed to obscure the historical background. Lake Edward had a Nilotic fish fauna throughout the Pleistocene period, and the fauna is still essentially Nilotic despite its truncated and impoverished species list.

This conclusion is not in accordance with WORTHINGTON's classification, in which he allies the Victoria and Edward faunal types as distinct from the Nilotic. However, the palaeontological evidence, as well as the relationships of the present-day fishes (excepting *Haplochromis*), both emphasise the Nilotic affinities of Lake Edward.

There remains one other much debated point on which the fossils throw some light. This concerns the thesis that certain predatory fishes, particularly *Lates* and *Hydrocyon*, have had an inhibiting effect on speciation and adaptive radiation amongst the smaller cichlids in lakes where these species occur together (*vide* WORTHINGTON, 1940; also MAYR, 1952, for criticism).

WORTHINGTON's ideas were apparently supported by the adaptively multiradiate *Haplochromis* species flocks of Lakes Edward and Victoria, lakes in which *Lates* had not been present for some considerable time (WORTHINGTON, 1940, and 1954). However, it is now known that *Lates* inhabited the Lake Edward basin until as recently as the early Holocene. This is turn implies that the ancestral *Haplochromis* species, or, small species flock, coexisted with *Lates* (see above, p. 71). Yet, this species flock, although smaller than that of Lake Victoria, is one cited by WORTHINGTON as an example of speciation unretarded by the influence of large predatory species.

At first sight this observation seems to tell against WORTHINGTON's general views on the overall retarding influence of *Lates* on adaptive

Period		Site	*Lepidosirenidae*	*Characidae*	*Cyprinidae*
HOLOCENE		ISHANGO; Z.POST-EM. Mesolithic (Site X a+X b+X c)	*Protopterus* sp.	—	*Barbus* sp.
EPI- PLEISTOCENE		ISHANGO; N.F.PR. Main fossiliferous level (Site IX)	*Protopterus* cf. *aethiopicus*	—	*Barbus* cf. *bynni* *Barbus* cf. *altianalis*
		ISHANGO; G.INF. Lower gravels (Site VIII b+VIII c)	*Protopterus* cf. *aethiopicus*	—	—
MIDDLE- PLEISTOCENE		27-30 m	—	—	—
		KATANDA AMONT 23 m (Site VI+VII)	—	—	*Barbus* sp.
LOWER PLEISTOCENE	THIRD KAISO LEVEL	KASAKA-SENGA (Site IV+V)	—	—	—
		Between ISHANGO and KANYATSI (Site V a)	—	*Hydrocyon* sp.	—
		KATANDA AVAL (Site III)	—	—	—
	FIRST KAISO LEVEL	KANYATSI (Site I+II)	*Protopterus* sp.	*Hydrocyon* sp.	—

Clariidae	Mochocidae	Bagridae	Centropomidae	Cichlidae
Clarias sp.	*Synodontis* cf. *frontosus*	*Bagrus* sp.	*Lates* sp.	*Tilapia* sp.
? *Heterobranchus* *Clarias lazera* *Clarias mossambicus*	*Synodontis* cf. *schall* *Synodontis* cf. *frontosus*	—	*Lates* cf. *niloticus*	*Tilapia* sp.
Clarias cf. *lazera* *Clarias* cf. *mossambicus*	*Synodontis* cf. *frontosus*	*Clarotes* sp.	*Lates* sp.	*Tilapia* sp.
—	*Synodontis* sp.	—	*Lates* sp.	—
Clarias sp.	*Synodontis* sp.	? *Clarotes* sp.	—	—
—	*Synodontis* sp.	? *Auchenoglanis* sp. (*Bagrus*, very dubious)	*Lates* sp.	—
—	—	—	*Lates* sp.	—
—	—	*Clarotes* sp. (*Bagrus*, very dubious)	—	—
Clarias sp.	*Synodontis* sp.	*Clarotes* sp. *Bagrus* sp. *Auchenoglanis* sp.	*Lates* cf. *niloticus*	(*Tilapia* sp., very dubious)

speciation. However, WORTHINGTON's conclusions were based on the assumption that *Lates* would eliminate those forms which passed through stages of imperfect adaptation in the course of evolution, and particularly those species attempting to colonize new adaptive niches. As the Lake Edward *Haplochromis* flock was apparently derived from an already multiradiate group in Lake Victoria, many invading species would be prospectively adapted to particular niches and might therefore be less affected by the presence of *Lates*.

Recent field studies on some of the African species flocks (FRYER and ILES, 1955; GREENWOOD, unpublished) show that WORTHINGTON underestimated the effect that other predatory species (for example, *Clarias*, *Bagrus* and *Barilius*) could have had on the development of cichlid species flocks. Since these other predators are associated with the flocks whose multiplicity of species was attributed to the absence of *Lates*, it is unlikely that predation did have such far-reaching inhibitory effects as WORTHINGTON postulated. Likewise, the demonstrated occurrence of *Lates* in the late Pleistocene Lake Edward, and its presumed coexistence with a developing *Haplochromis* species flock, helps to place the evolutionary significance of *Lates* in a truer perspective. *Lates* can only be considered as one of the many environmental factors which moulded the remarkable species flock of Lake Edward.

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BIBLIOGRAPHY.

ARAMBOURG, C., 1947, Mission Scientifique de l'Omo 1932-1933, t. I, fasc. 3 (Paris, éd. du Muséum, 57, rue Cuvier).

BEAUCHAMP, R. S. A., 1946, Lake Tanganyika (*Nature*, vol. CLVII, p. 193).

BROOKS, J. L., 1950, Speciation in ancient lakes (*Quart. Rev. Biol.*, XXV, pp. 31-176).

DE HEINZELIN, J., 1955, Le fossé tectonique sous le parallèle d'Ishango [*Inst. des Parcs Nationaux du Congo Belge*, Explor. du Parc Nat. Albert, Mission J. DE HEINZELIN DE BRAUCOURT (1950), fasc. 1].

FISH, G. R., 1956, Some aspects of the respiration of six species of fish from Uganda (*Journ. Exp. Biol.*, vol. XXXIII, pp. 186-195).

FRYER, G. and ILES, T. D., 1955, Predation pressure and evolution in Lake Nyasa (*Nature*, vol. CLXXVI, p. 407).

FUCHS, V. E., 1934, The geological work of the Cambridge Expedition to the East African lakes, 1930-1931 (*Geol. Mag.*, vol. LXXI, pp. 97-112, 145-166, pl. V, VI).

— 1936, Extinct Pleistocene molluscs from Lake Edward, Uganda, and their bearing on the Tanganyika problem (*J. Linn. Soc. London*, vol. XL, pp. 93-106, pl. I-III).

GREENWOOD, P. H., 1951 A, Evolution of the African cichlid fishes : the *Haplochromis* species-flock in Lake Victoria (*Nature*, vol. CLXVII, pp. 19-20).

— 1951 B, Fish remains from Miocene deposits of Rusinga island and Kavirondo Province, Kenya [*Ann. Mag. Nat. Hist.*, (12), vol. IV, pp. 1192-1201, pl. XXI].

HULOT, A., 1956, Aperçu sur la question de la pêche industrielle aux lacs Kivu, Édouard et Albert (*Bull. Agric. Congo Belge*, vol. XLVII).

MAYR, E., 1942, Systematics and the origin of Species (Columbia).

MORTELMANS, G., 1950, Le Quaternaire de l'Afrique sud-équatoriale. Essai de corrélation (*IIIe Congrès Nat. des Sciences*, Bruxelles, 1950).

O'BRIEN, T. P., 1939, Prehistory of Uganda Protectorate (Cambridge).

POLL, M., 1939, Poissons [*Inst. des Parcs Nationaux du Congo Belge*, Explor. du Parc Nat. Albert, Mission G. F. DE WITTE (1933-1935), fasc. 24].

POLL, M. and DAMAS, H., 1939, Poissons [*Ibid.*, Explor. du Parc Nat. Albert, Mission H. DAMAS (1935-1936), fasc. 6].

SOLOMON, J. D., 1939, in : *Prehistory of Uganda Protectorate* (see O'BRIEN).

TREWAVAS, E., 1933, Scientific results of the Cambridge Expedition to the East African lakes, 1930-1931. II : The cichlid fishes [*J. Linn. Soc. (Zool.)*, vol. XXXVIII, pp. 309-341].

— 1937, Fossil cichlid fishes of Dr. L. S. B. LEAKEY's Expedition to Kenya in 1934-1935 [*Ann. Mag. Nat. Hist.*, (10), vol. XIX, p. 381].

WAYLAND, E. J., 1931, Summary Progress Geol. Survey Uganda (Entebbe).

— 1934, Rifts, rivers, rains and early man in Uganda (*Journ. Roy. Anthrop. Inst.*, vol. LXIV, pp. 333-352, pls).

WAYLAND, E. J. and OTHERS, 1926, The Geology and palaeontology of the Kaiso Bone Beds (*Geol. Survey of Uganda*, pp. 1-71).

WHITE, E. I. and OTHERS, 1926, The Geology and palaeontology of the Kaiso Bone Beds (*Ibid.*, pp. 49-51).

WORTHINTGON, E. B., 1932, The lakes of Kenya and Uganda (*Geogr. Journ.*, vol. LXXIX, pp. 278-297, pl.).

— 1937, On the evolution of fish in the great lakes of Africa (*Inst. Rev. Hydrobiol. Leipzig*, vol. XXXV, pp. 304-317, map.).

— 1940, Geographical differentiation in fresh waters with special reference to fish, in : *The New Systematics*, pp. 287-302, Oxford.

— 1954, Fresh water organisms (*Proc. Linn. Soc. London*, vol. 165, Pt. I, pp. 68-74).

PLATE I

EXPLANATION OF PLATE 1.

Site I. — *Lates* sp.

1. 1st vertebra anterior face (0.8 ×).
2. 1st vertebra, left lateral view (0.8 ×).
3. 2nd vertebra, right lateral view (0.7 ×).
4. 3rd vertebra, right lateral view (0.8 ×).
5. 8th or 9th abdominal vertebra, lateral view (0.8 ×).
6. Caudal vertebra, right lateral view (0.9 ×).
7. Neurocranium right lateral view (0.4 ×).

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Exploration du Parc National Albert
Mission J. de HEINZELIN (1950), Fasc. 4.

Pl. I

P. H. GREENWOOD. — Quaternary Fish-fossils.

PLATE II

EXPLANATION OF PLATE II.

Site I. — *Lates* sp.

1. Ethmoid-vomer, left lateral view (0.8 ×).
2. Ethmoid-vomer, ventral view (0.9 ×).
3. 3rd and 4th vertebrae, right lateral view (0.8 ×).
4. Penultimate and ultimate abdominal vertebrae. lateral view (0.7 ×).
5. Caudal vertebra, lateral view (0.9 ×).
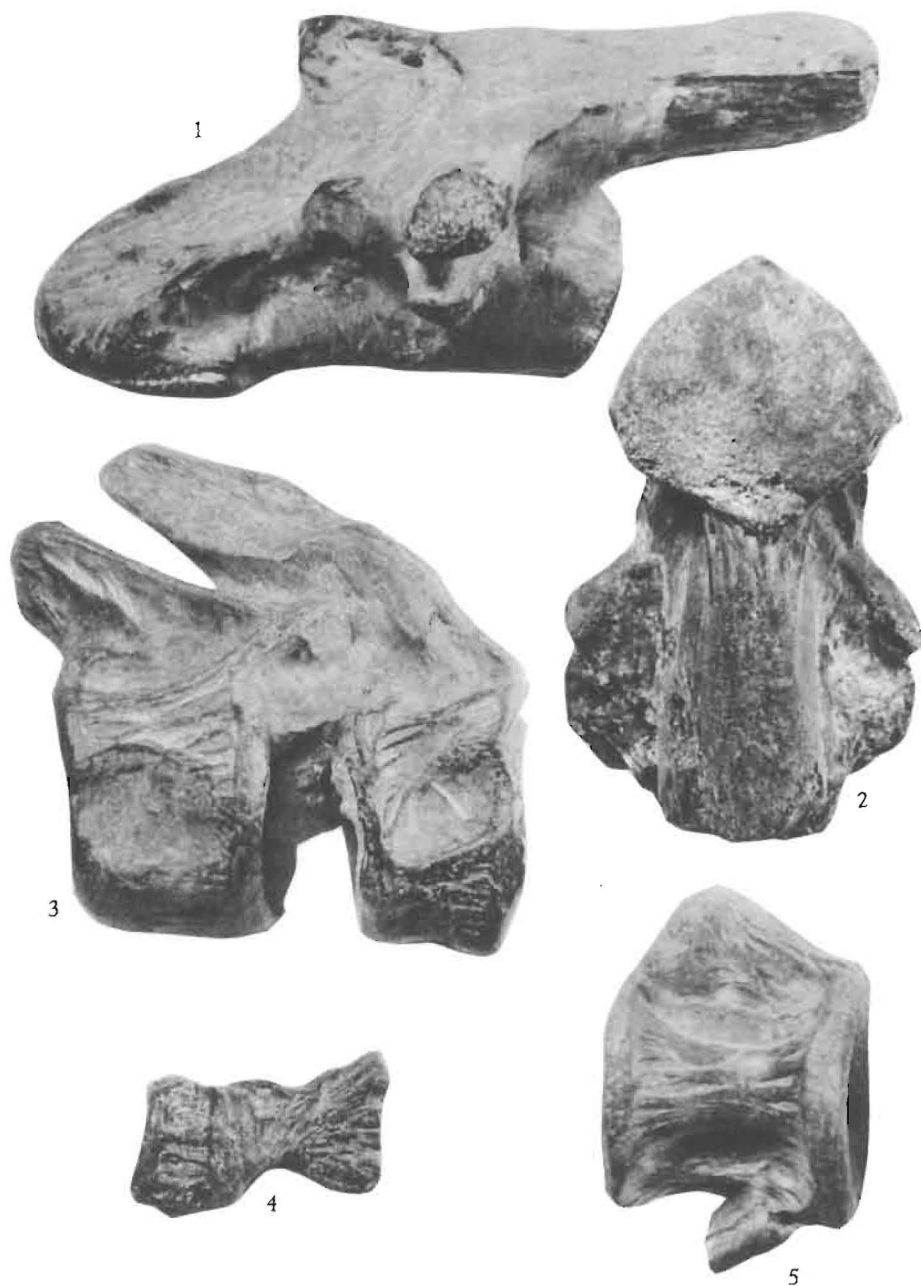
P. H. GREENWOOD. — Quaternary Fish-fossils.

PLATE III

EXPLANATION OF PLATE III.

Site I. — *Lates* sp.

1. Right articular, lateral view (0.8 ×).
2. Left cleithrum, lateral view (0.7 ×).
3. Right premaxilla, lateral view (0.8 ×).
4. Left quadrate, medial aspect (0.7 ×).
5. Right dentary, lateral aspect (0.8 ×).
6. Right ectopterygoid, ventral view (0.8 ×).
7. Left preoperculum, lateral view (0.7 ×).

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Exploration du Parc National Albert
Mission J. de HEINZELIN (1950), Fasc. 4.

Pl. III

P. H. GREENWOOD. — Quaternary Fish-fossils.

PLATE IV

EXPLANATION OF PLATE IV.

Site I (figs. 1 and 2). — Site II (figs. 3-6).

1. *Bagrus* sp. occipital region of skull, dorsal view.
2. *Idem*, left lateral view (0.85 ×).
3. *Lates*, 1st vertebra anterior face (0.8 ×).
4. *Lates*, 2nd vertebra anterior face (1.0 ×).
5. *Lates*, basioccipital and first vertebra, right lateral view (0.8 ×).
6. *Lates*, vomer, ventral face (0.95 ×).

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Exploration du Parc National Albert
Mission J. de HEINZELIN (1950), Fasc. 4.

Pl. IV
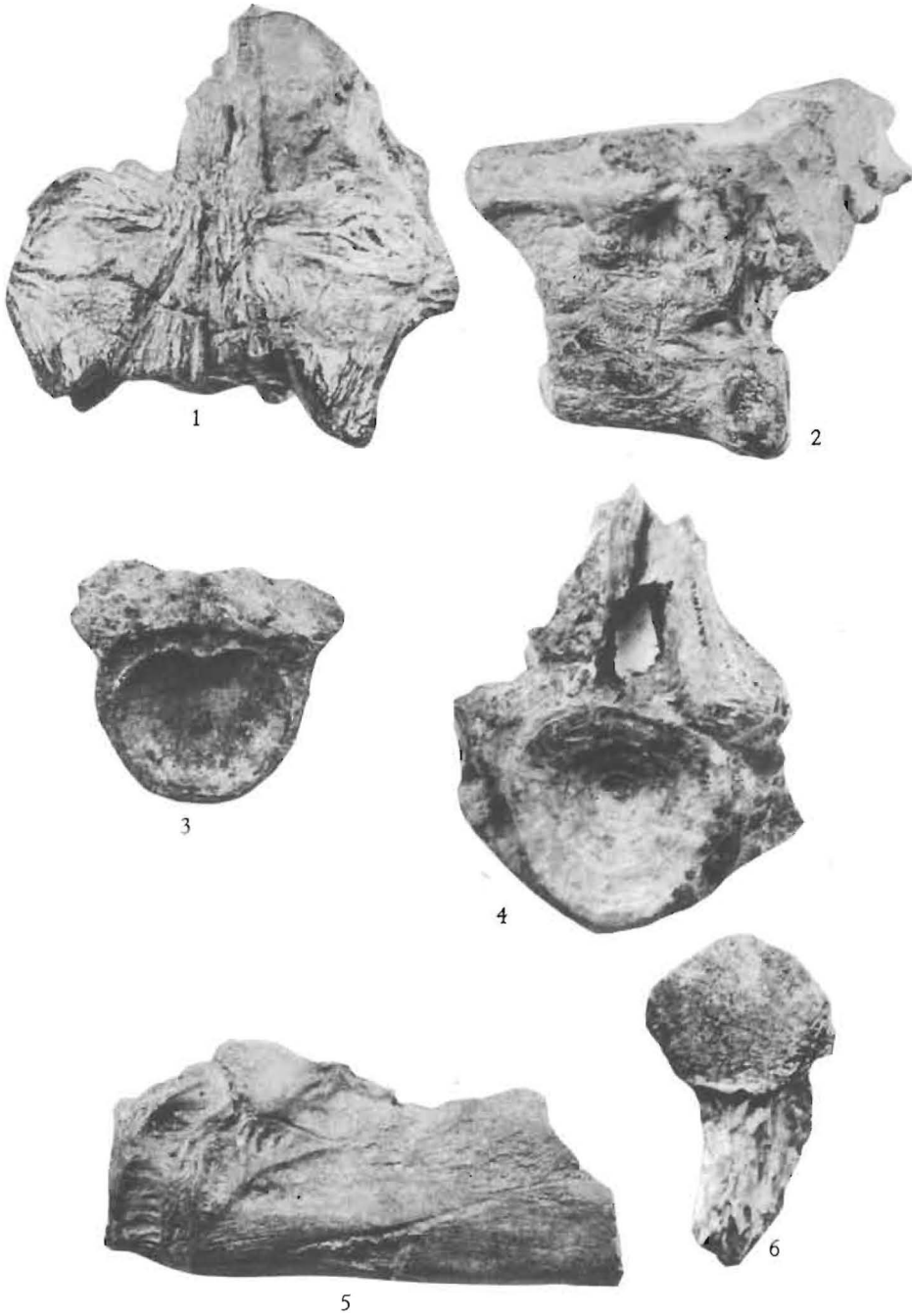
P. H. GREENWOOD. — Quaternary Fish-fossils.

PLATE V

EXPLANATION OF PLATE V.

Site I (figs. 1-10). — Site IV (fig. 11). — Site V (figs. 12-14).

1 and 2. *Clarotes* sp. pectoral spine, anterior and posterior faces .(0.8 ×).

3 and 4. *Auchenoglanis* sp., dorsal spine, anterior and posterior faces (0.8 ×).

5 and 6. *Tilapia* sp. 1st anal pterygiophore (both 0.8 ×).

7. *Bagrus* sp., fused anterior vertebral mass, lateral view (0.8 ×).

8. *Bagrus* sp., dermethmoid, dorsal view (0.8 ×).

9 and 10. *Auchenoglanis* sp.. pectoral spine, anterior and posterior faces (0.8 ×).

11. *Lates* sp., gillraker (0.7 ×).

12. *Lates* sp., 1st vertebra, anterior face (0.9 ×).

13. *Lates* sp., abdominal vertebra, lateral view (0.8 ×).

14. *Auchenoglanis* sp., left humeral process. lateral aspect (0.8 ×).

15. *Auchenoglanis* sp.. pectoral spine, posterior face (0.9 ×).

INSTITUT DES PARCS NATIONAUX DU CONGO BELGE
Exploration du Parc National Albert
Mission J. de HEINZELIN (1950), Fasc. 4.

Pl. V
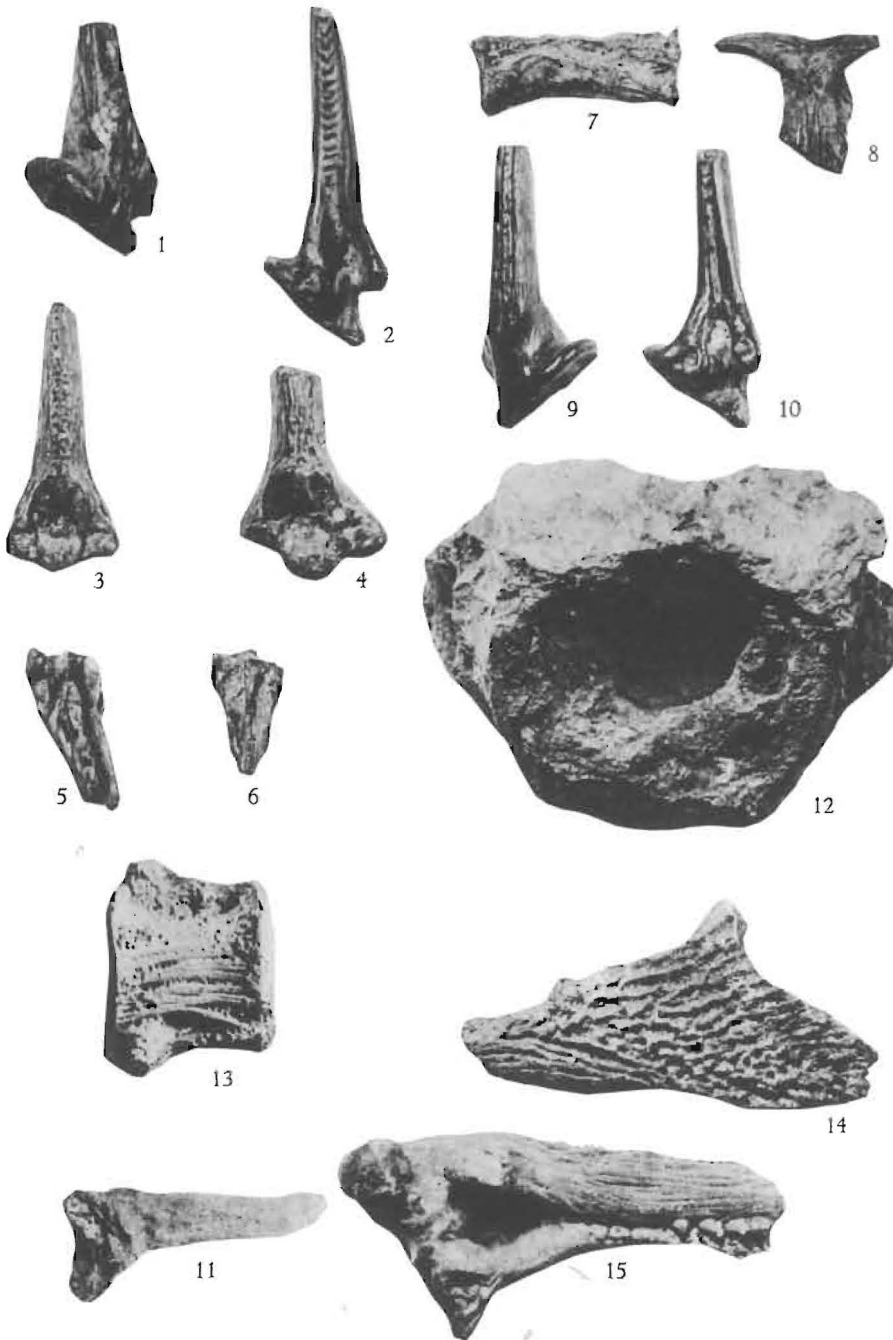
P. H. GREENWOOD. — Quaternary Fish-fossils.

PLATE VI

EXPLANATION OF PLATE VI.

Site VIII *a*.

    1 and 2. *Clarotes* sp., pectoral spine, dorsal and posterior faces (1.5 ×).

    3. *Protopterus* sp., left mandibular tooth-plate, lateral aspect (1.5 ×).

    4. Fragment of Clariid neurocranium (1.5 ×).

P. H. GREENWOOD. — Quaternary Fish-fossils.

PLATE VII

EXPLANATION OF PLATE VII.

Site VIII *b* (figs. 1, 5 and 7). — Site VIII *c* (figs. 2-4, 6-8).

1. *Lates* sp., Abdominal vertebra, oblique lateral view (1.7 ×).
2. *Lates* sp., dentary, medial aspect (1.6 ×).
3. *Lates* sp., left preoperculum, lateral aspect (1.1 ×).
4. *Lates* sp., ectopterygoid, ventral aspect (1.2 ×).
5. *Barbus* sp., abdominal vertebra, lateral view (1.6 ×).
6. *Synodontis* sp., pectoral spine, dorsal and posterior aspects (1.6 ×).
7. *Synodontis* sp., pectoral spine, dorsal aspect (1.6 ×).
8. *Synodontis* sp., left humeral process, lateral aspect (1.8 ×).

INSTITUT DES PARCS NATIONAUX DU CONGO BELGE
Exploration du Parc National Albert
Mission J. de HEINZELIN (1950), Fasc. 4.

Pl. VII
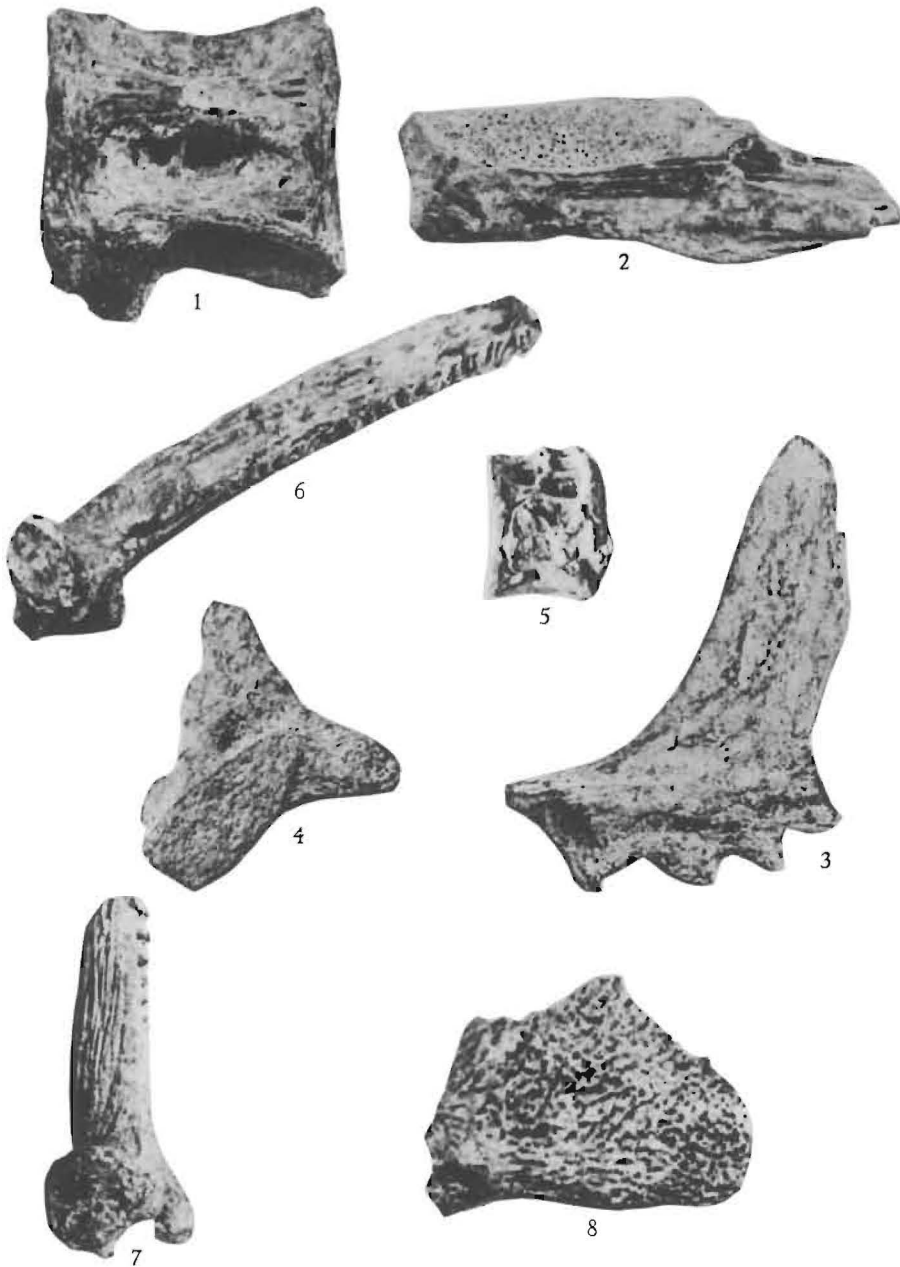
P. H. GREENWOOD. — Quaternary Fish-fossils.

PLATE VIII

EXPLANATION OF PLATE VIII.

Barbus sp. or spp. (see text p. 42).

1 and 2. Right operculum, lateral and medial aspects (0.5 ×).

3. Left hyomandibular, lateral aspect (0.5 ×).

4. Right quadrate, medial aspect (0.6 ×).

5. Fragment of pharyngeal bone, showing major pharyngeal tooth (0.6 ×).

6. Entire pharyngeal bone (right), medial aspect (0.65 ×).

7. Left dentary, lateral aspect (0.65 ×).

8. Fragment of pharyngeal bone, showing major pharyngeal tooth (0.75 ×).

9. Fragment of right dentary (0.75 ×).

10 and 11. 3rd interneural pterygiophore, posterior and anterior faces (0.6 ×).

12 and 13. 3rd interneural pterygiophore, anterior and posterior faces (0.6 ×).

14 and 15. 1st interneural pterygiophore, anterior and lateral aspects (0.65 ×).

16 and 17. 1st and 2nd vertebrae (0.4 ×).

18 and 19. Caudal veretbrae (0.4 ×).

20. Abdominal vertebra (0.8 ×).

21. Caudal vertebra (0,8 ×).

INSTITUT DES PARCS NATIONAUX DU CONGO BELGE
Exploration du Parc National Albert
Mission J. de HEINZELIN (1950), Fasc. 4.

Pl. VIII
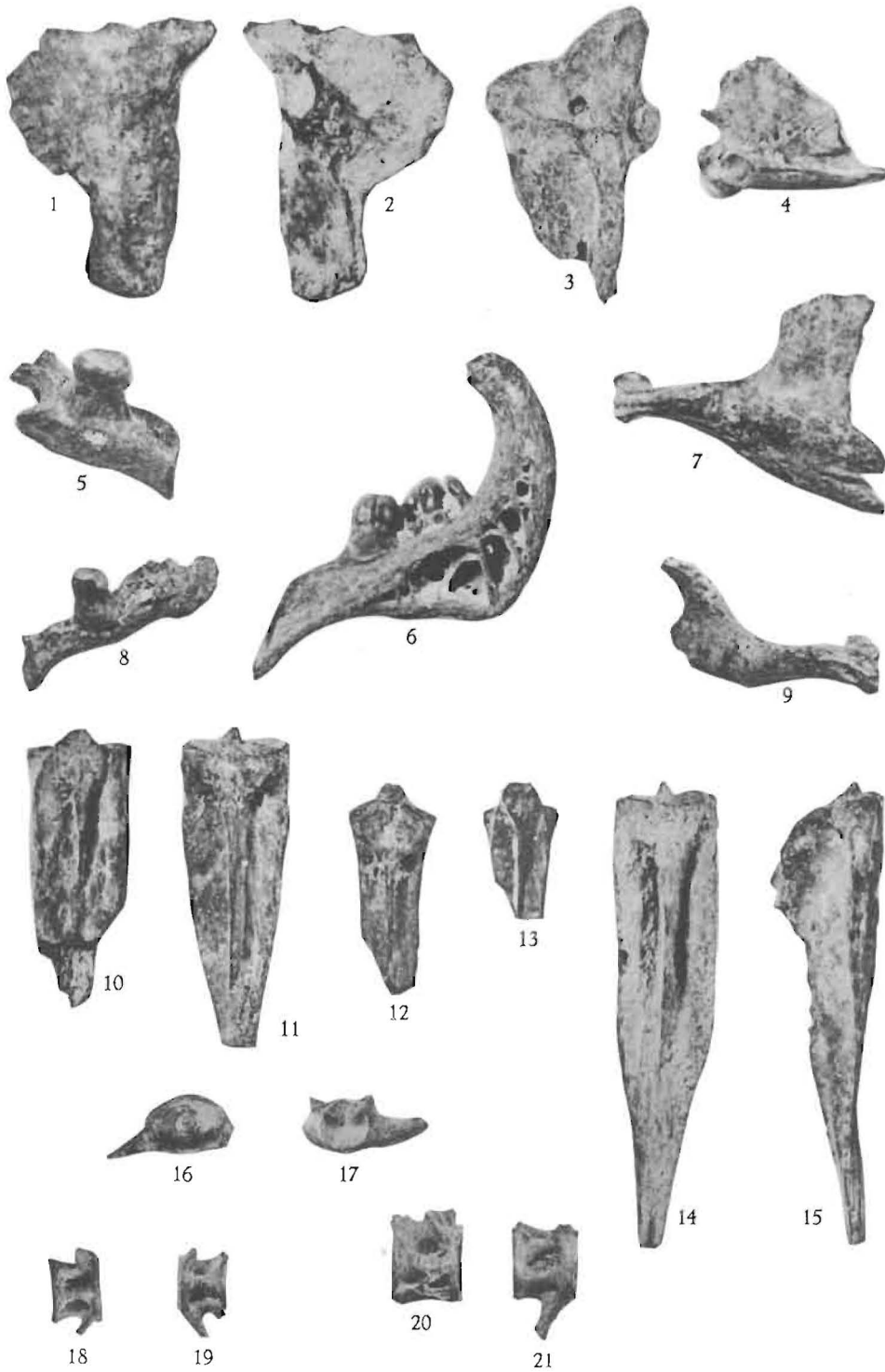
P. H. GREENWOOD. — Quaternary Fish-fossils.

PLATE IX

EXPLANATION OF PLATE IX.

Site IX. — *Synodontis frontosus* (figs. 1-12) and ? *Heterobranchus* sp. (figs. 13 and 14).

1. Supraoccipital, dorsal view (1.2 ×).

2 and 3. Left and right frontal (from different individuals) (1.2 ×).

4. Occipito-nuchal plate, dorsal view (1.2 ×).

5. Ethmoid, dorsal view (1.25 ×).

6 and 7. Left and right humeral process and cleithrum (left 1.3 ×, right 1.2 ×).

8. 2nd dorsal spine, anterior aspect (1.2 ×).

9 and 10. 3rd dorsal spine lateral and anterior aspects (anterior 1.2 ×, lateral 1.0 ×).

11 and 12. Anterior abdominal vertebrae (1.0 ×).

13. ? *Heterobranchus* sp., ? post-temporal, dorsal view (1.0 w).

14. ? *Heterobranchus* sp., frontal, dorsal view (1.0 ×).

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Exploration du Parc National Albert
Mission J. de HEINZELIN (1950), Fasc. 4.

Pl. IX
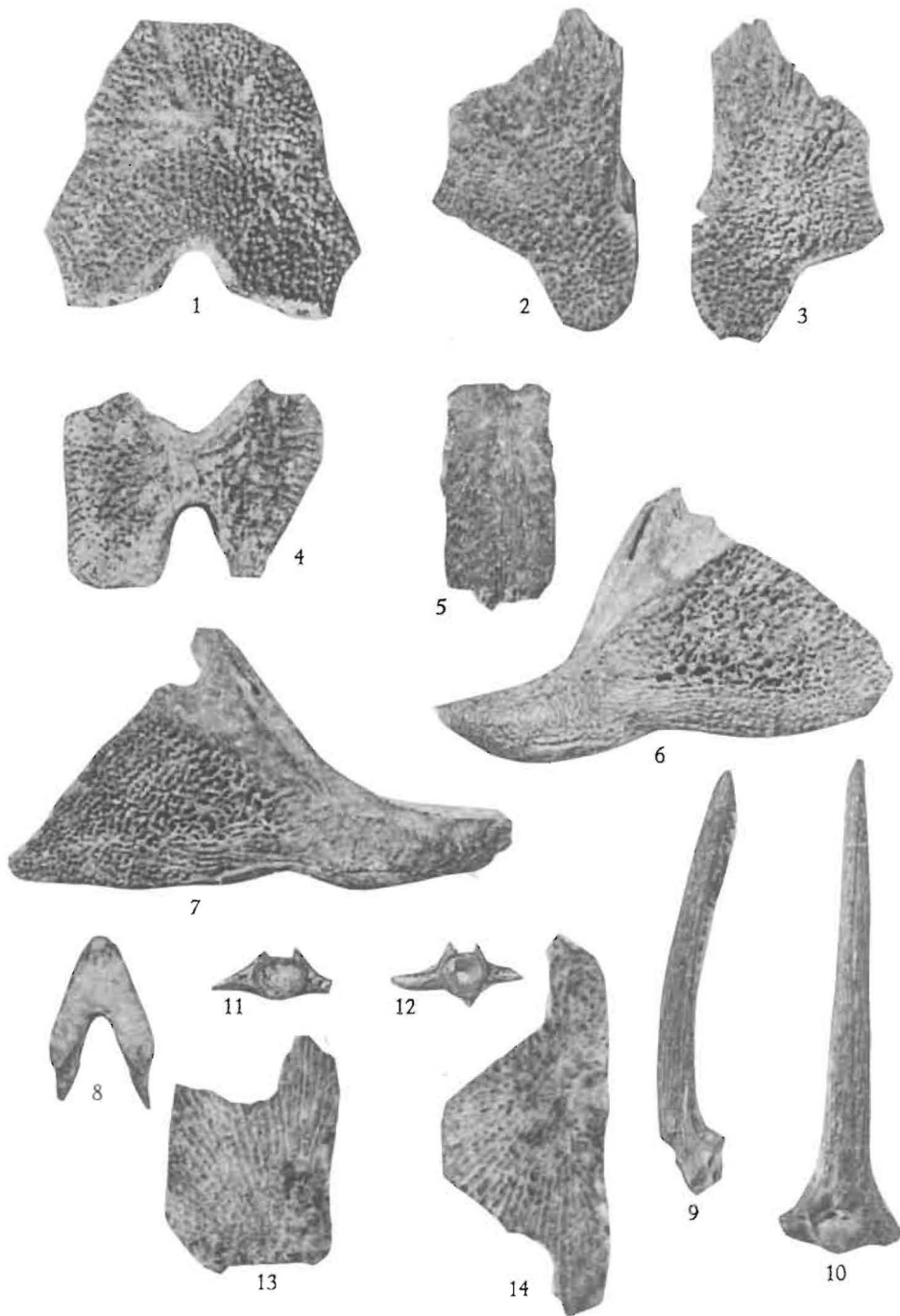
P. H. GREENWOOD. — Quaternary Fish-fossils.

PLATE X

EXPLANATION OF PLATE X.

Site IX. — *Clarias* cf. *C. lazera.*

1. Supra-orbital, dorsal view (1.2 ×).
2. Prefrontal, dorsal view (1.2 ×).
3. Frontal, dorsal view (1.0 ×).
4. Urohyal, ventral aspect (1.5 ×).
5. Supraoccipital, dorsal view (1.3 ×).
6. Dermethmoid, dorsal view (1.2 ×).
7. Fragment of cleithrum, ventro-lateral aspect (1.0 ×).
8. Epi- and ceratohyal, ventral aspect (1.0 ×).

INSTITUT DES PARCS NATIONAUX DU CONGO BELGE
Exploration du Parc National Albert
Mission J. de HEINZELIN (1950), Fasc. 4.

Pl. X
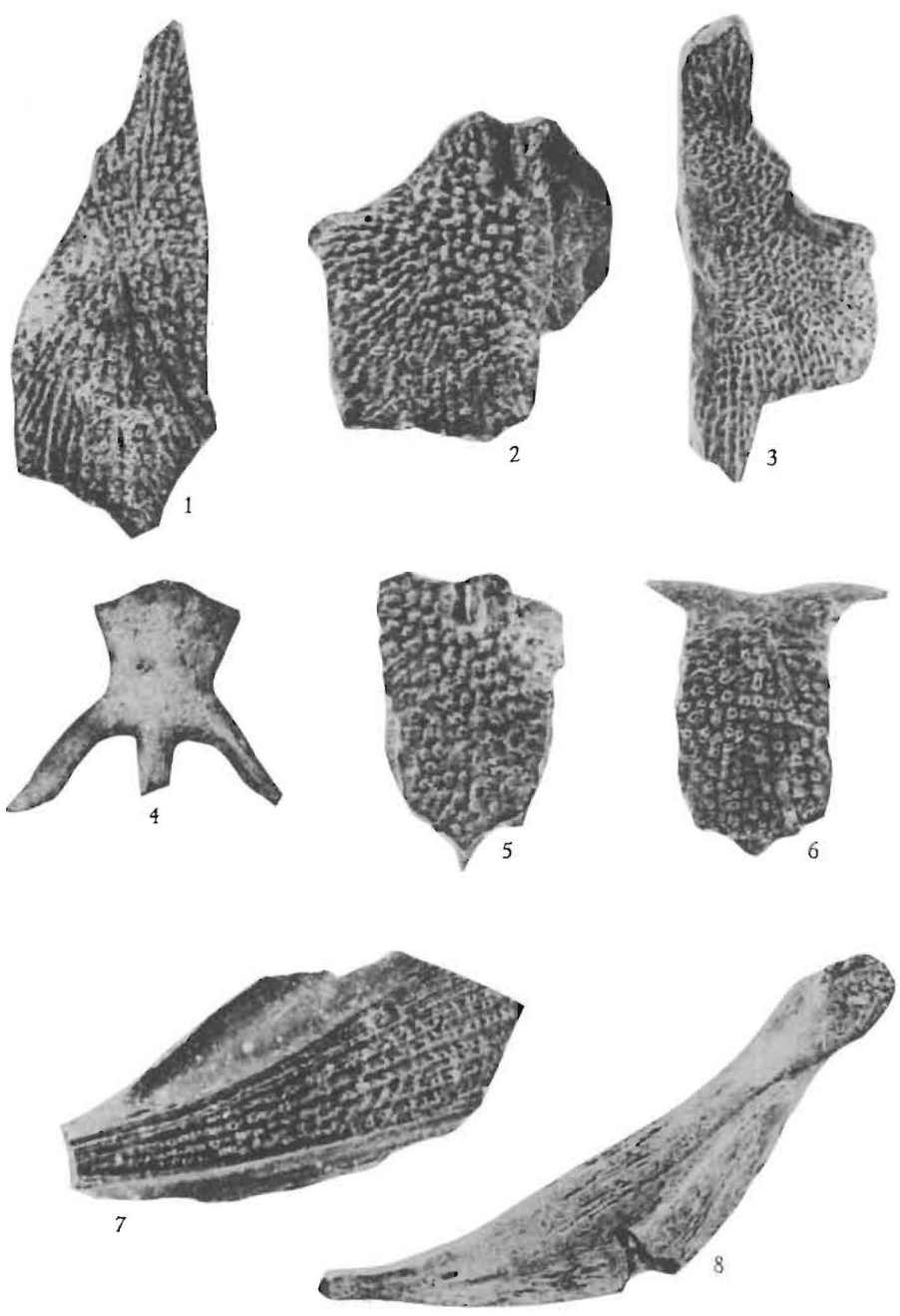
P. H. GREENWOOD. — Quaternary Fish-fossils.

PLATE XI

EXPLANATION OF PLATE XI.

Site IX. — *Lates* sp.

1. Quadrate, lateral aspect (0.8 ×).
2. 3rd vertebra, left lateral aspect (0.8 ×).
3. Right dentary, lateral aspect (0.75 ×).
4. 1st vertebra, right lateral aspect (0.8 ×).
5 and 6. Ventral view of vomerine tooth patch, showing variation in the shape of the posterior margin (both 0.8 ×).
7. Left preoperculum, medial aspect (0.8 ×).
8. 2nd vertebra, left lateral aspect (0.8 ×).
9 and 10. Caudal vertebrae (both 0.8 ×).
11. Right premaxilla, ventral aspect of dentigerous surface (0.8 ×).

INSTITUT DES PARCS NATIONAUX DU CONGO BELGE
Exploration du Parc National Albert
Mission J. de HEINZELIN (1950). Fasc. 4.

Pl. XI

P. H. GREENWOOD. — Quaternary Fish-fossils.

PLATE XII

EXPLANATION OF PLATE XII.

Site IX (figs. 1-8 and 11-12) and Site I (figs. 9-10).

1 and 2. *Tilapia* sp., 1st interhaemal pterygiophore, lateral aspect (both 1.2 ×).

3. *Tilapia*, left premaxilla lateral aspect (1.2 ×).

4. *Tilapia*, urohyal, left lateral aspect (1.2 ×).

5. *Tilapia*, 1st vertebra, anterior face (1.2 ×).

6. *Tilapia*, 2nd vertebra, anterior face (1.2 ×).

7. *Tilapia*, 3rd vertebra, anterior face (1.2 ×).

8. *Tilapia*, anterior abdominal vertebra, anterior face (1.0 ×).

9 and 10. *Protopterus* sp., upper and lower tooth-plates, right lateral aspect (0.7 ×).

11 and 12. *Protopterus* sp., upper and lower tooth-plates, right lateral aspect (0.8 ×).
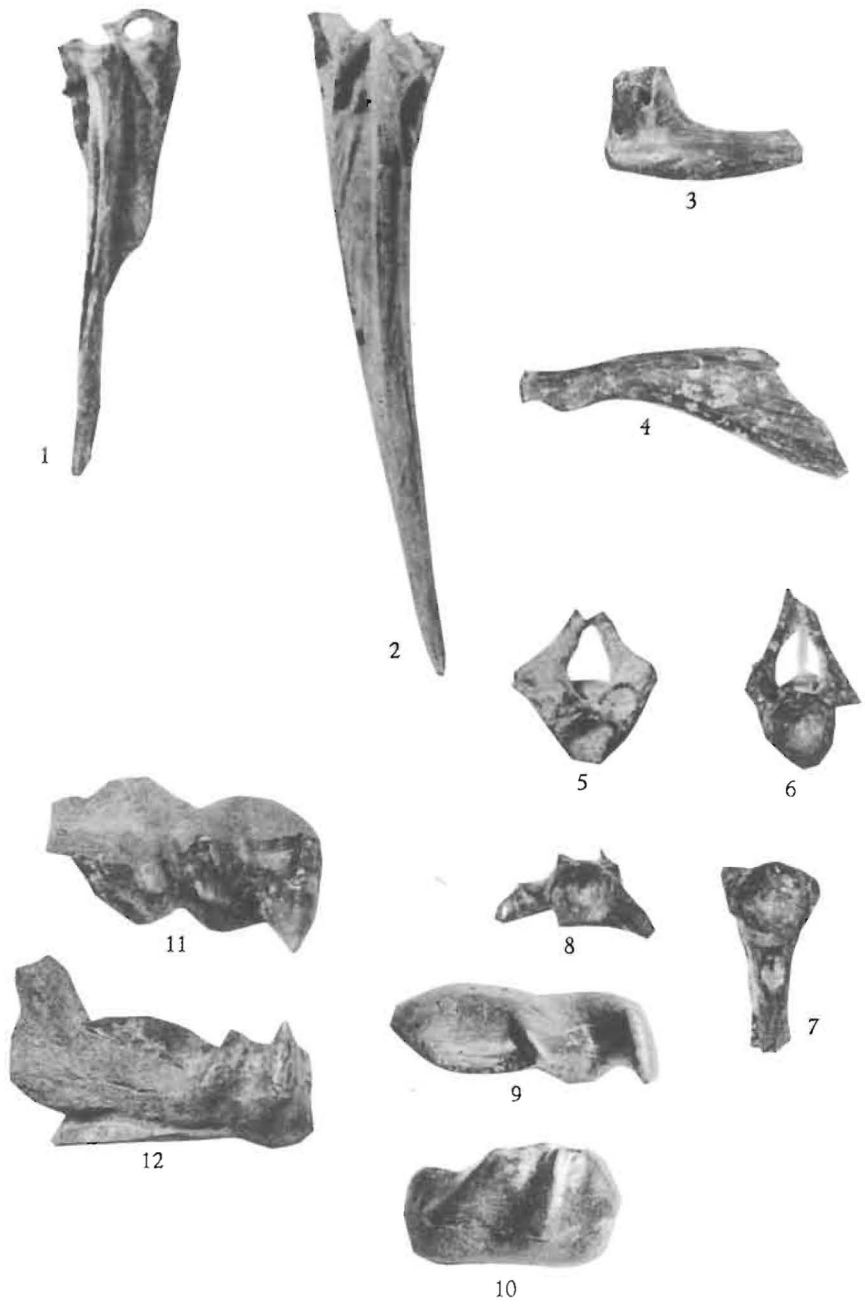
P. H. GREENWOOD. — Quaternary Fish-fossils.

PLATE XIII

EXPLANATION OF PLATE XIII.

Site X *a* (figs. 8 and 9). — Site X *b* (figs. 1-7).

1. *Clarias* sp., dermethmoid, dorsal view (1.5 ×).
2 and 3. *Clarias* sp., fragments of neurocranium (both 1.1 ×).
4 and 5. *Clarias* sp., abdominal and caudal vertebrae (both 1.6 ×).
6 and 7. *Tilapia* sp., 1st vertebrae, anterior and lateral aspects (1.6 × and 1.8 × respectively).
8. *Bagrus* sp., supraoccipital region of neurocranium, dorsal view (1.4 ×).
9. *Bagrus* sp., fragment of frontal, dorsal view (1.1 ×).
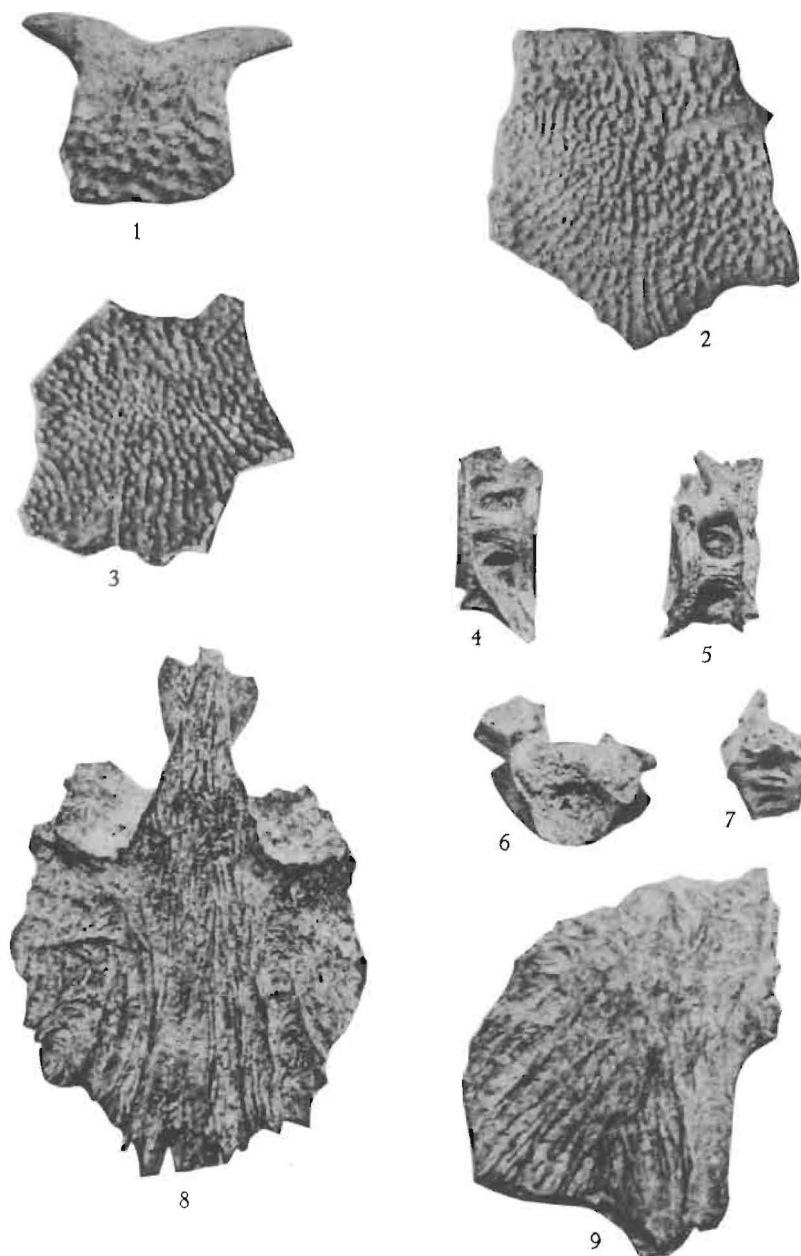
P. H. GREENWOOD. — Quaternary Fish-fossils.

PLATE XIV

EXPLANATION OF PLATE XIV.

Site X c.

1. *Bagrus* sp., basioccipital, ventral aspect (0.8 ×).
2. *Bagrus*, supraoccipital, dorsal aspect (0.8 ×).
3. *Bagrus*, fused anterior vertebral mass, lateral view (0.8 ×).
4. *Bagrus*, post-temporal (0.8 ×).
5. *Bagrus*, abdominal vertebra, lateral view (0.8 ×).
6. *Bagrus*, pectoral spine, anterior view (0.8 ×).
7. *Bagrus*, right articular, lateral aspect (0.8 ×).
8. *Bagrus*, right dentary, viewed obliquely from above (0.8 ×).
9. *Bagrus*, caudal vertebrae, lateral view (0.8 ×).
10. *Clarias* sp., prefrontal, dorsal view (0.8 ×).
11 and 12. *Clarias*, fragments of neurocranium. dorsal view (both 0.8 ×).
13. *Clarias*, pectoral spine, antero-dorsal aspect (0.9 ×).
14. *Clarias*, dermethmoid dorsal view (0.9 ×).
15 and 16. *Barbus* sp., caudal vertebrae, lateral aspect (0.9 ×).
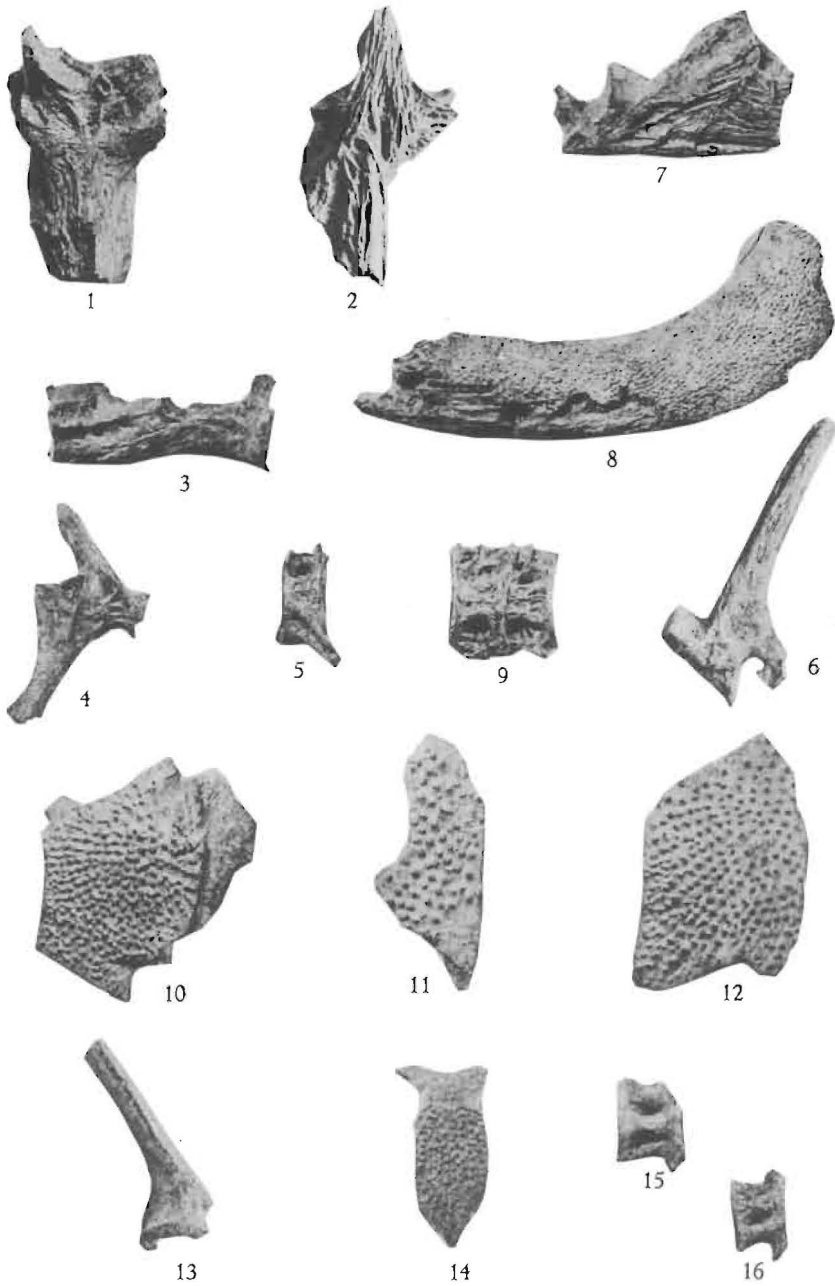
P. H. GREENWOOD. — Quaternary Fish-fossils.

OISEAUX FOSSILES

PAR

René VERHEYEN (Bruxelles)

Tous les débris fossiles que nous avons identifiés proviennent du gisement d'Ishango et en majorité du niveau fossilifère principal N.F.PR. Bon nombre de restes osseux restent à déterminer, mais nous ne disposons pas encore des documents ostéologiques de comparaison qui seraient nécessaires. Nous croyons toutefois qu'il s'agit toujours d'espèces qui sont encore représentées aujourd'hui au même endroit.

La présence d'un fragment d'œuf d'autruche retient toutefois l'attention. Il se rapporte à la sous-espèce *massaicus*, autrefois abondante dans le Kenya. Il est donc probable que cette sous-espèce avait une répartition plus étendue en Uganda et jusqu'aux abords d'Ishango, à moins que le fragment d'œuf ait été importé. De toute façon, on peut présumer que la différenciation géographique de l'espèce *Struthio camelus* était déjà accomplie il y a sept ou huit mille ans, au moment de la civilisation d'Ishango. Il serait intéressant de comparer les fragments d'œufs d'autruche recueillis parmi les restes des civilisations d'affinités capsiennes, des civilisations de Karthoum et Shaheinab et des civilisations mésolithiques australes.

Espèces du niveau Z.POST-EM.

? *Platalea alba* (SCOPOLI) = spatule blanche.

? *Ardea melanocephala* (VIGORS et CHILDREN) = héron à tête noire; 2e métacarpien.

Espèces du niveau N.F.PR.

? Platalea alba (SCOPOLI) = spatule blanche.

? Ardea melanocephala (VIGORS et CHILDREN) = héron à tête noire.

Ibis ibis (L.) = ibis des bois; 2ᵉ métacarpien.

Leptoptilos crumeniferus (LESSON) = marabout; tibiotarse et humérus.

Ephippiorhynchus senegalensis (SHAW) = jaribu africain; tarso-métatarse.

Phalacrocorax carbo (L.) = cormoran noir d'Afrique; ulna, plusieurs méta-carpiens et humérus.

Pelecanus rufescens (GMELIN) = pélican rose; ulna.

Plectropterus gambensis (L.) = oie éperonnée; plusieurs exemplaires du 2ᵉ métacarpien, scapula et humérus, phalange basale du 3ᵉ doigt, ulna.

Cuncuma vocifer (DAUDIN) = aigle pêcheur; tarso-métatarse.

Struthio camelus massaicus (NEUMANN) = autruche du Kenya; fragment de coquille d'œuf.

MAMMIFÈRES FOSSILES

PAR

A. Tindell HOPWOOD (Londres) et Xavier MISONNE (Bruxelles)

Le matériel que nous avons étudié provient du gisement d'Ishango et a été recueilli pour la plus grande part en 1950 au cours de la Mission J. DE HEINZELIN. Nous y avons adjoint quelques spécimens recueillis en 1935 par H. DAMAS au cours d'un premier sondage.

Les notations stratigraphiques dont nous faisons usage se rapportent toutes à la publication de J. DE HEINZELIN (¹). Les niveaux fossilifères étudiés sont de haut en bas, dans l'ordre de superposition stratigraphique :

Habitats récents = BANTOU, C.V., Z.N., POT. de la coupe figurée.

Ossements de teinte brune à brun rouge pâle, friables à l'intérieur.

Habitats mésolithiques = Z.POST-EM., zone postérieure à l'émersion définitive de la terrasse.

Ossements de teinte brune à brun gris ou brun chocolat, légèrement lapidifiés.

Niveaux tufacés = P.G.A., P.G.B., S.P., B.C., G.H. de la coupe figurée, correspondent sur l'ancienne berge du lac aux accumulations de cendres volcaniques subaériennes qui couvrent les topographies plus élevées.

Ossements de teinte brun jaune, brun gris à brun sombre, très lapidifiés, non colorés à l'intérieur; ils sont souvent encroûtés de telle sorte dans le matériel tufacé qu'ils cassent au cours de l'extraction.

Niveau fossilifère principal = N.F.PR. = gisement-type de l'Homme d'Ishango.

(¹) J. DE HEINZELIN DE BRAUCOURT, 1957, Les fouilles d'Ishango (*Inst. des Parcs Nationaux du Congo Belge*, Mission J. DE HEINZELIN DE BRAUCOURT, fasc. 2).

On y a adjoint les restes de vertébrés de G.Y., S.X., S.INF. et G.X. de la coupe figurée.

Ossements très lapidifiés, sonnant au choc, de teinte brun violacé à noirâtre, colorés à l'intérieur.

Gravier inférieur = G.INF., base de la terrasse, probablement de nature fluviale.

Ossements très roulés, à surface poreuse et mate lorsqu'ils sont autochtones et à surface lisse, plus pesants et plus compacts lorsqu'ils sont remaniés de formations plus anciennes.

Les ossements sont si morcelés que, pour la plupart, leur détermination reste toujours incertaine sinon impossible. Il y en a quelques-uns néanmoins dont l'identité n'est pas douteuse et qui suffisent à indiquer la composition de la faune de l'époque. Cette faune n'est cependant pas connue dans son entièreté, car les fossiles ne sont que les restes d'animaux de chasse; les autres tels que petits rongeurs, insectivores, carnivores et périssodactyles y manquent complètement ou à peu près.

1. HABITATS RÉCENTS.

Les débris d'ossements récents sont pratiquement inexistants en surface. Seuls peuvent être recueillis des débris enfouis sous des colluvions de surface ou dans des excavations anciennes (trous de pieux, détritus). Ils se mêlent le plus souvent alors aux débris de Z.POST-EM., et il n'est pas facile de les départager. Il nous suffira de citer les espèces qui apparaissent ou se répandent avec plus d'abondance parmi ces déchets récents :

Potamochoerus cf. *porcus.* — Très rare, une troisième molaire du niveau de 0-25 cm de Il. DAMAS [2].

Kobus defassa (RUPPELL). — Très rare hors de ces déchets récents où il devient assez commun. Phalanges, os du carpe et du tarse.

2. ZONE POST-ÉMERSION = Z.POST-EM.

Colobus sp. — Une molaire inférieure.

Panthera pardus (L.). — Partie proximale d'un cubitus.

Hystrix sp. — Une molaire.

Dendrohyrax sp. — Fragment d'un rameau horizontal mandibulaire avec les dents molaires.

Hippopotamus amphibius L. Commun. Dents, os des membres, du carpe, du tarse et de la colonne vertébrale.

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[2] Cf. aussi N.F.PR.

Phacochoerus aethiopicus (PALLAS). — Assez rare : 6 molaires et quelques fragments.

Damaliscus lunatus (BURCHELL). — Espèce la plus commune de tous les grands mammifères : chevilles osseuses, dents, os.

Cephalophus sp. — Espèce de grande taille : cheville osseuse, dents, petits os du carpe et du tarse. Assez rare.

Redunca redunca (PALLAS). — Assez rare : cheville osseuse, molaires, astragales.

Tragelaphus scriptus (PALLAS). — Assez rare : molaires, astragales.

Syncerus caffer (SPARRMAN). — Assez rare : astragales, quelques molaires.

S. nanus (BODDAERT). — Assez commun : prémolaires, molaires, os des membres.

Outre les débris autochtones qui viennent d'être cités, le niveau d'occupation recélait une molaire de *Stegodon kaisensis* HOPWOOD, certainement originaire de la Série de Kaiso et une molaire d'*Hippotigris* sp., elle aussi vraisemblablement originaire de la Série de Kaiso ou de la Semliki. L'état de fossilisation de la molaire de *Stegodon* ne laisse aucun doute quant à son origine tandis que celui de la molaire d'*Hippotigris* paraît plus jeune, analogue même à la fossilisation autochtone.

3. NIVEAUX TUFACÉS.

Lycaon pictus (TEMMINCK). — Très rare : une molaire inférieure. Collection DAMAS; à 2,50 m de profondeur.

Hippopotamus amphibius L. — Commun : dents et os.

Phacochoerus arthiopicus (PALLAS). — Très rare : moitié postérieure d'une troisième molaire.

Damaliscus lunatus (BURCHELL). — Assez commun : chevilles osseuses, dents, os de membres.

Redunca redunca (PALLAS). — Très rare : cheville osseuse.

Syncerus caffer (SPARRMAN). — Rare : astragale, épiphyse distale d'un canon.

S. nanus (BODDAERT). — Rare : astragale, petit os du carpe, phalange proximale.

4. NIVEAU FOSSILIFÈRE PRINCIPAL = N.F.PR.

Lutra maculicollis LICHTENSTEIN. — Rare : deux pièces de mâchoire inférieure, l'une d'elles avec la carnassière.

Lepus cf. *victoriae*. — Assez rare; fragments de mâchoires.

Thryonomys swinderianus TEM. — Assez rare : palais, mâchoires inférieures, dents isolées.

Hippopotamus amphibius L. — Commun : dents et ossements.

Potamochoerus porcus (L.). — Rare : fragments de mâchoires juvéniles (d'un seul individu ?).

Phacochoerus aethiopicus (PALLAS). — Très rare : défense.

Damaliscus lunatus (BURCHELL). — Très commun : chevilles osseuses, dents, ossements.

Cephalophus sp. — Assez commun : grande espèce représentée surtout par des astragales dont quelques-uns pourraient être rapportés à un tragélaphe d'une taille plus petite que la moyenne.

Redunca redunca (PALLAS). — Rare : cheville osseuse, quelques dents de lait.

Tragelaphus scriptus (PALLAS). — Rare : cheville osseuse, astragale, calcanéum.

Syncerus caffer (SPARRMAN). — Assez commun : dents, astragales, calcanéum, fragments des os longs.

S. nanus (BODDAERT). — Un peu moins commun que le précédent : dents, petits os du carpe et tarse et d'autres ossements.

5. GRAVIERS INFÉRIEURS = G.INF.

Il n'y a que très peu de mammifères fossiles autochtones dans les graviers inférieurs et leurs restes épars ne donnent qu'une idée qualitative de la faune. La détermination de l'hippopotame est basée sur trois, et celle du phacochère sur deux dents; toutes les autres sont fondées chacune sur un seul spécimen.

Lutra maculicollis (LICHTENSTEIN). — Mâchoire inférieure droite.

Hippopotamus amphibius L. — Trois dents.

Phacochoerus aethiopicus (PALLAS). Deux dents.

Alcelaphus lelwell (HEUGLIN). — Cheville osseuse.

Kobus ? — Troisième molaire inférieure.

Syncerus caffer (SPARRMAN). — Fragment de la moitié proximale du métacarpe.

Outre les débris autochtones qui viennent d'être cités, le gravier inférieur recélait un grand nombre de débris osseux remaniés de la Série de Kaiso, qui affleure sous la terrasse et recèle non loin de là d'importants bancs fossilifères. Les os sont souvent usés au point de n'être plus que des cailloux osseux. Nous avons pu toutefois identifier :

Hippopotamus grandeur *H. amphibius*, peut-être *H. gorgops* DIETRICH.

Phacochoerus sp.

Antilopes, deux espèces indéterminées.

LA FAUNE ACTUELLE.

La vallée de la Semliki est connue par les nombreuses récoltes faites dans le Parc National Albert. La connaissance des Mammifères actuels de cette région est basée sur les publications et listes d'H. SCHOUTEDEN (1935), G. F. DE WITTE (1937), S. FRECHKOP (1938, 1943, 1944), E. HUBERT (1947), R. HOIER (1950, 1952), ainsi que sur une liste manuscrite de W. HAYMAN (1945). Plusieurs conversations avec S. FRECHKOP nous ont permis de préciser ces connaissances. Les régions biogéographiques sont connues par la carte de W. ROBYNS (1947). Enfin l'écologie et l'éthologie des espèces se trouvant dans le Parc National Albert ont été décrites dans les travaux d'E. HUBERT (1947), H. HEDIGER (1951), R. VERHEYEN (1951) et R. HOIER (1952).

Toutes ces études permettent une bonne compréhension de la faune. Les cartes pluviométriques de la région (F. BULTOT, 1950) complètent la documentation.

Les plaines du lac Édouard sont moins arrosées que les régions avoisinantes. La vallée de la Haute-Semliki se présente comme une savane bordée de montagnes. Elle ne communique de façon directe avec d'autres régions de savane que par l'est et tout d'abord avec la plaine du lac George (Katwe, bord du Toro). Les monts Bukuku ne sont pas un obstacle pour la faune et même les hippopotames y voyagent de nuit régulièrement. Plus loin, le Kazinga Channel sépare la région de Katwe du Bunyarunguru (côte orientale du lac) auquel fait suite le Kigezi et les plaines des Rwindi-Rutshuru (côte méridionale du lac).

Vers le nord, la plaine de la Haute-Semliki va s'enfoncer entre la crête Congo-Nil, la grande forêt ombrophile de la Basse-Semliki et le massif du Ruwenzori. La côte occidentale du lac, quoique très montagneuse n'est pas un obstacle absolu au passage de la faune car on y rencontre des éléphants, des antilopes et des buffles. La faune n'est donc isolée par des barrières écologiques que vers le nord.

Les données quantitatives concernant la faune ne sont guère abondantes. E. HUBERT donne quelques indications sur la région s'étendant au sud du lac, partie très sèche; ces indications peuvent nous donner une idée approximative de la proportion des différentes espèces d'antilopes.

	1930	1941
Damaliscus	10.000	1.200
Adenota kob	15.000	3.000
Kobus defassa	1.000	700
Redunca redunca	1.000	800
Tragelaphus scriptus	500	500

Le même auteur donne également la densité par km² pour quelques espèces : lion : 1 pour 5 km²; léopard : 1 pour 12 km²; hyène tachetée : 1 pour 4 km²; éléphant : 1 pour 8 km²; phacochère : 1 par km²; potamo-

chère : moins dense que le phacochère; hylochère : 1 pour 6 km²; *Damaliscus* : 12 par km²; *Kobus defassa* : 1 par km²; *Adenota kob* : 24 par km²; *Redunca redunca* : 2 par km²; *Tragelaphus scriptus* : 1 pour 2 km²; *Syncerus caffer* : 3 pour 2 km².

COMPARAISON AVEC LA FAUNE FOSSILE D'ISHANGO.

Étant donné qu'il s'agit de restes de cuisine nous n'aurons qu'une idée approximative de la faune. Les insectivores, cheiroptères, primates, carnivores et rongeurs seront rares ou absents.

A première vue, la faune ancienne n'est guère différente de la faune d'aujourd'hui. Nous pouvons cependant mettre quelques faits en évidence.

Parmi les antilopes, le Topi, *Damaliscus lunatus*, autrefois si commun, est absent aujourd'hui; il est vrai qu'il pullule dans la réserve du lac George, à quelque 50 km d'Ishango, ainsi qu'au sud du lac Édouard. Cette espèce, très sédentaire (H. HEDIGER, 1951), a pu disparaître localement, à la suite d'une épidémie ou autre cause, sans qu'elle ait jamais recolonisé.

Adenota kob, aujourd'hui commun, est complètement absent comme fossile.

Alcelaphus lelwell, dont nous ne possédons qu'une cheville osseuse appartenant incontestablement à cette espèce, n'existe pas actuellement dans le Parc National Albert. On le trouve cependant dans le Parc National de la Kagera (Coll. Inst. Parcs Nat.) et au nord de la Semliki (liste de W. HAYMAN), soit à 100 ou 130 km d'Ishango. Il est possible que cette espèce ait eu autrefois une dispersion plus grande.

Kobus defassa, aujourd'hui commun, est inexistant jusqu'aux couches contemporaines de la culture bantoue où il devient abondant. Il n'occupait vraisemblablement pas la région avant cette époque.

Redunca redunca, actuellement commun, est rare ou absent à tous les niveaux fossilifères.

Tragelaphus scriptus, actuellement commun, est plutôt rare parmi les fossiles.

Syncerus nanus et *S. caffer* : il est intéressant de remarquer que le buffle nain semble être plus abondant que le grand buffle. Le premier est forestier, le second habite la savane. Le buffle nain ne se rencontre aujourd'hui que très exceptionnellement dans la région.

Le groupe des suidés (*Potamochoerus*, *Phacochoerus*, *Hylochoerus*) montre quelques caractéristiques : le potamochère est très rare parmi les fossiles. Cette espèce est aujourd'hui toujours associée aux cultures; les populations d'Ishango vivant surtout de chasse et de pêche, les cultures devaient être réduites, d'où le faible nombre de potamochères. Le phacochère est représenté en proportion normale comme fossile, tandis que l'hylo-

chère est absent. Cette espèce habite en lisière des forêts; on l'a toujours cru rare, il semble pourtant qu'il n'en soit pas ainsi : un chasseur officiel a été chargé de réduire le nombre de suidés dans la région du Parc National Albert et ses captures, de février 1945 à juin 1946, se répartissaient de la façon suivante : 329 potamochères, 619 hylochères, 77 phacochères (R. Hoier, 1952). Disons toutefois que dans la région même d'Ishango, le phacochère prédomine encore de loin aujourd'hui.

Hippopotamus est très abondant à tous les niveaux, comme encore aujourd'hui. Il devait constituer, avec *Damaliscus*, la nourriture principale des populations d'Ishango.

Lutra maculicollis n'a été signalé que dans la baie de Sake (lac Kivu), elle se trouve également plus au nord, comme l'atteste un crâne provenant de la Semliki dans les collections de l'Institut des Parcs Nationaux du Congo Belge. Les riverains pêcheurs du lac Édouard devaient capturer de temps à autre une loutre. Son absence des niveaux supérieurs peut être considérée comme accidentelle.

Panthera pardus est représenté par un cubitus. La densité actuelle d'un léopard pour 12 km² correspond aux chances que nous avions de le rencontrer parmi les fossiles.

Thryonomys est le seul rongeur présent. La population actuelle ne le mange pas, mais les tribus voisines le considèrent comme excellent.

L'absence des éléphants est un fait assez curieux. *Loxodonta africana* est aujourd'hui très commun. Il est possible que les indigènes de l'époque ne le chassaient pas.

Lycaon, *Dendrohyrax* et *Lepus* cf. *victoriae* nous fournissent seulement la preuve de leur existence ancienne dans la région.

Il est à remarquer que la girafe (*Giraffa camelopardalis* L.) ne se rencontre ni à l'état fossile ni actuellement dans la vallée de la Semliki. Elle y a cependant existé : le Dr Parke, qui accompagnait Stanley lors de l'expédition lancée au secours d'Emin Pacha, dit avoir vu des antilopes et des girafes dans la vallée, mais qu'aucune n'a survécu à l'épidémie qui suivit.

Il faut remarquer que les espèces de forêts sont mieux représentées qu'actuellement à la fois dans la zone post-émersion et le niveau fossilifère principal. *Cephalophus sylvicultor*, par exemple, n'a été signalé qu'à Mutsora (Ruwenzori, secteur nord du Parc). De même, la présence de *Syncerus nanus* en nombre plus important, de *Colobus polykomos* essentiellement forestier et arboricole, l'absence d'*Adenota*, le petit nombre de *Redunca* semble indiquer une plus grande extension de la végétation forestière.

Les spécimens de la faune des niveaux tufacés sont réduits en nombre et ont relativement peu de signification. Cette faune a dû subir des conditions de vie très spéciales au moment de la précipitation des cinérites.

L'extension du couvert forestier dans la plaine de la Haute-Semliki doit avoir pour cause un facteur climatique, probablement une plus grande pluviosité. Deux éventualités sont possibles, par rapport au climat actuel :

a) Une augmentation absolue du volume des précipitations annuelles;

b) Une répartition plus régulière des pluies, qui se répartissent aujour-d'hui en orages rares et violents.

Sur la carte pluviométrique de F. BULTOT, Ishango est situé dans la zone de 1.200 mm de précipitation annuelle, alors que les forêts, à quelque 40 ou 50 km de ce point, suivent assez exactement la courbe de 1.300 mm de précipitation.

En l'absence de stations d'observations régulières ces données n'ont qu'une valeur d'estimation. Elles indiquent cependant qu'il ne faut pas imaginer de variation climatique considérable pour justifier une légère extension de la végétation forestière.

CONCLUSIONS.

Deux espèces étaient abondantes et formaient le fond de la nourriture des populations anciennes d'Ishango : *Hippopotamus* et *Damaliscus*. Ce dernier a disparu localement.

Au point de vue biogéographique, l'ensemble de la faune a plus d'affi-nités forestières et de lisières de forêts que la faune actuelle, ce qui n'est explicable que par une végétation ligneuse plus dense à l'époque.

Kobus defassa s'est introduit à une époque récente dans la région tandis qu'*Alcephalus* se rencontrait durant la période la plus ancienne de la for-mation de la terrasse et a disparu. On ne voit pas trace de périssodactyles, zèbre et rhinocéros, ni de girafe, comme encore aujourd'hui. Les restes d'Ishango ne renferment pas non plus d'ossements d'éléphant, qui n'était peut-être pas chassé, ou rarement.

La faune des Mammifères dans son ensemble n'a pas subi de grands changements, sinon dans la proportion des espèces représentées.

BIBLIOGRAPHIE.

BULTOT, F., 1950, Régimes normaux et cartes de précipitations dans l'Est du Congo Belge (*Publ. I.N.É.A.C.*, Bruxelles, Bur. clim., comm. n° 1).

— 1950, Carte des régions climatiques du Congo belge (*Ibid.*, comm. n° 2).

FRECHKOP, S., 1938, Exploration du Parc National Albert. Mission G. F. DE WITTE. 10 : Mammifères (*Inst. Parcs Nationaux du Congo Belge*, Bruxelles, pp. 1-103).

— 1938, Exploration du Parc National Albert. Mission S. FRECHKOP. Mammifères (*Ibid.*, Bruxelles, pp. 1-186).

— 1938, Exploration du Parc National de la Kagera. Mission S. FRECHKOP. I : Mammifères (*Ibid.*, Bruxelles, pp. 1-56).

HEDIGER, H., 1951, Observations sur la psychologie animale, fasc. 1 (*Ibid.*, Bruxelles, pp. 1-194).

HOIER, R., 1950, A travers plaines et volcans au Parc National Albert (*Ibid.*, Bruxelles, pp. 1-172).

— 1950, Mammifères du Parc National Albert (*Office de Publicité*, Bruxelles, pp. 1-107.)

HOPWOOD, A. T., 1926, The Geology and Palaeontology of the Kaiso bone-bed. I : Mammalia (*Geol. Survey Uganda*, Occasional papers, n° 2, pp. 13-36).

HUBERT, E., 1947, La faune des grands Mammifères de la plaine Rwindi-Rutshuru (lac Edouard). Son évolution depuis sa protection totale (*Inst. Parcs Nationaux du Congo Belge*, Bruxelles, pp. 1-84).

MISONNE, X., 1952, Quelques éléments nouveaux concernant *Hippopotamus imaguncula* (*Bull. Inst. Roy. Sc. Nat. Belg.*, t. XXVIII, 3, pp. 1-12).

PITMAN, 1953, The balance of Nature (*Oryx*, V, 2, n° 1, p. 11).

ROBYNS, W., 1947, Les territoires biogéographiques du Parc National Albert (*Inst. Parcs Nationaux du Congo Belge*).

SCHOUTEDEN, H., 1935, Les Mammifères du secteur septentrional du Parc Albert (Kivu) (*Rev. Zool. Bot. Afric.*, V, XXVI, pp. 202-210).

VERHEYEN, R., 1951, Contribution à l'étude éthologique des Mammifères du Parc National de l'Upemba (*Inst. Parcs Nationaux du Congo Belge*, Bruxelles).

WITTE, G. F., DE, 1937, Exploration du Parc National Albert. I : Introduction (*Ibid.*, Bruxelles, pp. 1-39).

TABLE GÉNÉRALE DES MATIÈRES