

# NEW CROCODILES FROM THE EARLY MIOCENE OF KENYA

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**ABSTRACT.** An almost complete crocodile skull was found by the British-Kenya Miocene Expedition in the Fossil Bed Member of the Hiwegi Formation, at Kaswanga, Rusinga Island, Kenya in 1948. This is the most complete specimen from the Early Miocene deposits of East Africa. This skull, which superficially resembles that of *Crocodylus niloticus*, actually belongs to a new, relatively small species of *Crocodylus*. Fragmentary material of a crocodile similar to *C. niloticus* occurs at almost all of the Early Miocene sites in East Africa. Although disarticulated skull and postcranial remains from the same stratigraphic horizon and a partial skull from the Kulu Formation of Rusinga Island can be referred to this new species with some assurance, the remaining material cannot.

A mandibular fragment of a long-snouted form, cf. *Euthecodon* sp., is known from the Early Miocene Gumba Red Beds of Rusinga Island, and elongate teeth, possibly referable to this genus, are known from the Early Miocene Karungu Beds. These represent the earliest appearance of the genus *Euthecodon* and are the only longirostrine crocodiles known from any Early Miocene deposits in Africa.

FRAGMENTARY remains of crocodiles similar to *C. niloticus* have been found in almost all of the Early Miocene fossil-bearing deposits of East Africa. The best specimen is a nearly complete skull from the Lower Miocene Fossil Bed Member of the Hiwegi Formation. This was discovered in 1948 by the British-Kenya Miocene Expedition led by Louis Leakey at Kaswanga, Rusinga Island, Kenya (34° 21' E., 0° 25' S.). This skull, and disarticulated skull material and postcrania collected in 1967 from the same horizon by Van Couvering, are described below as a new species of *Crocodylus*. Comparative material studied by Tchernov is listed in Table 1. The material described here is housed either in the British Museum (Natural History) (BMNH) or the Kenya National Museum (KNM).

## SYSTEMATIC PALAEOLOGY

Genus *CROCODYLUS* Laurenti, 1798

*Crocodylus pigotti* sp. nov.

Plate 99; text-fig. 1

**Derivation of name.** Named for D. B. Pigott, who was eaten by a crocodile during his return from a fossil collecting expedition to the Early Miocene beds at Karungu, Kenya in 1909 (cf. Clark and Leakey 1951, for further details).

**Diagnosis.** *Crocodylus* with fairly flat, low skull, slender at quadratojugal level; moderately long, narrow rostrum due to slight increase in relative length of premaxillae and maxillae relative to primitive crocodylids such as *C. megarhinus*. Paramedian premaxillary-maxillary suture extends posteriorly to level of second maxillary tooth. Facial process of premaxilla extends to level of second maxillary tooth. Maxillo-palatine median suture extends to level between seventh and eighth maxillary teeth. Palatine fenestra small with anteriormost margins at level of tenth maxillary tooth. Five premaxillary and fourteen maxillary teeth; premaxillary notch for lower canine noticeably constricted; large protuberance on rostrum immediately posterior to fifth maxillary tooth. Mandible with fifteen teeth.

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*Holotype.* Uncatalogued specimen, BMNH, R7729 (Field No. R65, 1948); an almost complete skull without lower jaw.

*Referred Material.* All referred material has prefix KNM-RU. The specimen number follows name of the bone. Complete left ulna (2560), complete right femur (2561), proximal right femur (2562), proximal right humerus (2563), distal right humerus (2564), complete right fibula (2565), proximal left coracoid (2566), two cervical vertebrae (2567-2568), dorsal vertebra (2570), sacral vertebra (2571), dorsal vertebra (2573), cervical vertebra (2574), frontoparietal (2575), right jugal (2576), left ectopterygoid (2577), basioccipital (2578), right jugal (2579), partial left dentary (2580), right surangular (2581), two partial right dentaries (2582-2583), right angular (2584), five scutes (2596), and one fragmentary right maxilla (2597).

*Horizon and Locality.* Below Marker Bed I, Fossil Bed Member, Hiwegi Formation; Shackleton Gully, Kaswanga, Rusinga Island, South Nyanza, Kenya.

*Age.* Early Miocene, about 17 M.y. (Van Couvering and Miller 1969).

*Description.* This is a relatively small species of *Crocodylus* with a moderately elongated rostrum as compared to primitive crocodylids such as *C. megarhinus*. This elongation is mainly due to the slight increase in the relative length of the premaxillae, but the maxillae are also slightly longer allowing enough room for a fourteenth permanent maxillary tooth. This appears only rarely in *C. niloticus*.

*Morphology.* The cranial table is nearly square, although slightly broader than long. In the type the left margin is broken away. The table is flat, although the rim of the supratemporal opening stands slightly above the general surface; the sides diverge posteriorly. The interorbital area is small and somewhat concave.

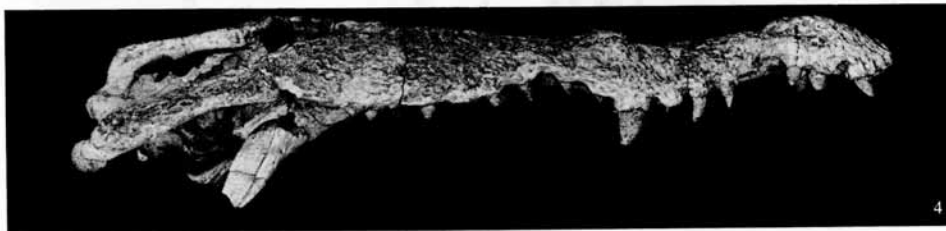
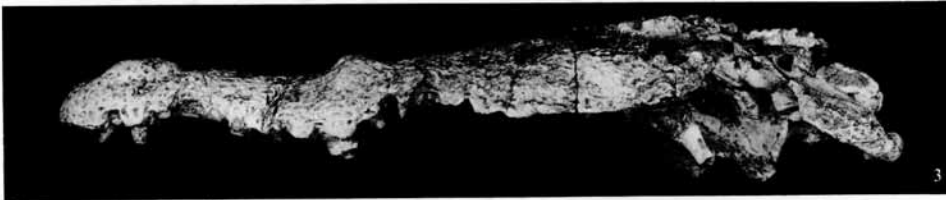
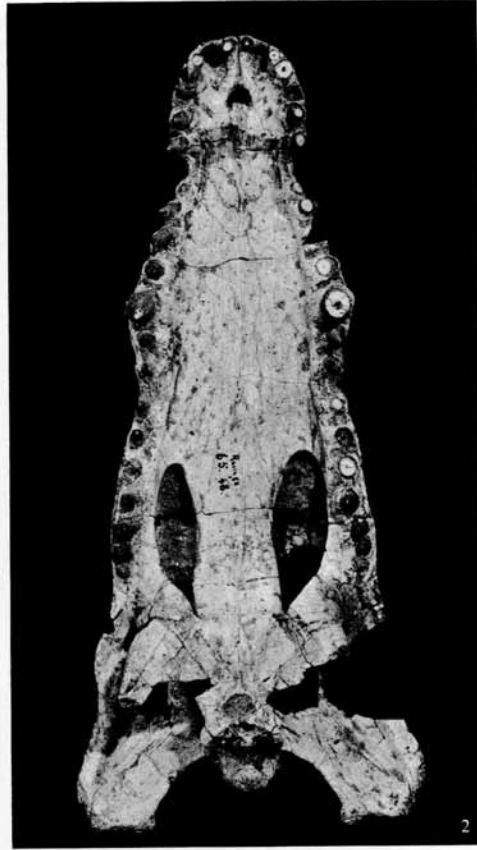
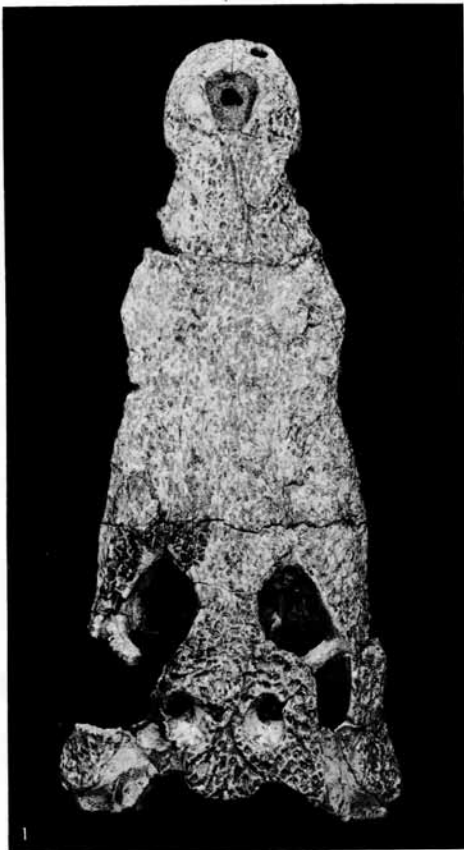
The supratemporal fenestrae are small and slightly longer than broad, with the anterior-posterior axis skewed slightly antero-laterally. The axis is in line with the inner margin of the orbit. The shape of the infratemporal fenestra cannot be determined as the quadratojugal is broken away anteriorly. The orbits are longer antero-posteriorly than transversely; the long axis is nearly parallel to the slightly raised orbital margins. The outer orbital rims are straighter than those of *C. niloticus*. The anterior end of the external narial opening is much broader than the posterior end, thus forming a triangle with the base anterior. The outer rims are straighter than in *C. niloticus*. The anterior end of the opening is at the level of the third premaxillary tooth; the posterior end is even with the fifth premaxillary tooth. The internal narial opening is broader than long, faces antero-ventrally and is much broader than in *C. niloticus*. The palatine fenestrae extend forward to the level of the anterior end of the tenth maxillary tooth. The anterior margins are rounded and the posterior margin is pointed medially. The right fenestra has been compressed.

Several sutural relationships are important (Table 1, text-fig. 1a). The paramedian premaxillary-maxillary suture extends posteriorly to the level of the second maxillary tooth, as in *C. niloticus* and *C. megarhinus* but further than in *C. lloidi* or *C. palustris*. The facial process of the premaxilla also extends to the level of the second maxillary tooth, much more anterior than in any of the species examined. The maxillo-palatine median suture extends to between the seventh and eighth maxillary teeth, further

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EXPLANATION OF PLATE 99

Holotype of *Crocodylus pigotti* (BMNH R7729) from the Fossil Bed Member, Hiwegi Formation, Rusinga Island, Kenya. Fig. 1, dorsal view. Fig. 2, ventral view. Fig. 3, left lateral view. Fig. 4, right lateral view. Scale in mm.



TCHERNOV and VAN COUVERING, Miocene crocodiles

TABLE 1. Selected morphological features of some species of *Crocodylus*.

	<i>C. megarhinus</i> (?Late Eocene, North Africa)	<i>C. iloidi</i> (Neogene and Lower Pleistocene of North and East Africa)	<i>C. sivalensis</i> (Pliocene, Siwalik Series, India)	<i>C. niloticus</i> (Plio-Pleistocene and Recent of East Africa)	<i>C. palustris</i> (Recent, India)	<i>C. pigotti</i> (Lower Miocene, Rusinga, Kenya)
1. Palatal suture of pre-maxillae-maxillae points to the level of . . .	2nd max. tooth	mid 1st max. tooth	end of 1st max. tooth	2nd max. tooth	end of 1st max. tooth	2nd max. tooth
2. Facial process of pre-maxilla extends back to the level of . . .	?4th max. tooth	4th max. tooth	4th max. tooth	between 4th-5th max. teeth	4th max. tooth	2nd max. tooth
3. Maxillo-palatine median suture extends to the level of . . .	between 8th-9th max. teeth	6th max. tooth	7th max. tooth	7th max. tooth	between 6th-7th max. teeth	between 7th-8th max. teeth
4. Anterior margin of palatine fenestra points to the level of . . .	anterior margin of 9th max. tooth	between 7th-8th max. teeth	7th max. tooth	between 8th-9th max. teeth	between 8th-9th max. teeth	10th max. tooth
5. Posterior extension of external narial opening lies . . .	anterior to notch	anterior to notch	—	even with notch	anterior to notch	anterior to notch
6. Posterior extension of jaw symphysis lies . . .	behind 5th mand. tooth	between 3rd-4th mand. teeth	—	behind 4th mand. tooth	4th mand. tooth	behind 5th mand. tooth
7. Number of pre-maxillary teeth	5	5	5	5	5	5
8. Number of maxillary teeth	13	14	14	13	13-14	14
9. Number of dentary teeth	15	15	—	15	14-15	15

back than in *C. niloticus*, *C. lloidi* and *C. palustris* but not so far as in *C. megarhinus*.

There is no complete mandible, but three large dentary fragments (KNM-RU 2580, 2582, 2583) show that there were fifteen mandibular teeth and that the splenial extended to the level of the posterior margin of the seventh alveolus, as in *C. niloticus*. The symphysis extended to the level of the posterior margin of the fifth alveolus. The internal foramen of the dentary is at a level between the alveoli of the thirteenth and fourteenth mandibular teeth.

*Proportions.* Table 2 gives the proportions of *C. pigotti*, *C. niloticus* and *C. lloidi*. The measurements of *C. pigotti* are given in Table 3. In general the skull proportions of *C. pigotti* are more similar to those of *C. niloticus* than to those of any other African *Crocodylus*, and it is much more elongate than the brevirostrine *C. lloidi*. Index 1 (the width of the skull across the anterior ends of the orbits relative to the width of the skull across the quadratojugals) is larger in *C. pigotti* than in *C. niloticus* and is well within the range of *C. lloidi*, the probable ancestor of *C. pigotti* (see below). The width of the skull across the fifth maxillary teeth ('canines') in *C. pigotti* well exceeds the range of *C. niloticus* (Index 2) and preserves the proportions of the extreme brevirostrine crocodile, *C. lloidi*. The premaxillae of *C. pigotti* are more elongate than those of *C. niloticus* (Index 3). *C. pigotti* has an extremely low skull (Index 4) which is not due to crushing (Plate 99). Though still within the range of *C. niloticus*, *C. pigotti* is characterized by a relatively narrow skull across the quadratojugals (Index 5) and a broader skull at the palatine level. Other differences from *C. niloticus* are given in Indices 7-10, Table 2. Assuming that the related parameters are fixed, Indices 8-10 show a noticeably low skull, elongated premaxillae and a relatively wide palate at the level of the fifth maxillary teeth.

*Discussion.* Text-fig. 1b clarifies the general differences in proportions between *C. pigotti* (inner continuous line) and *C. niloticus* (outer, broken line): elongated premaxillae; broader palate at the 'canine' level; slender skull at the quadratojugal level; differences in shape of palatal sutures, especially that of the maxillo-palatine and maxillo-premaxillae, and smaller size of the palatine fenestra. Together with the differences in the relationships between the palatal sutures to the maxillary teeth, these characters demonstrate the uniqueness of *Crocodylus pigotti*. Fragmentary specimens of disarticulated skulls and skeletons which were collected by Van Couvering at Kaswanga, Rusinga Island have been referred to this species. Although they are fragmentary, they appear to be disarticulated remains of a very few individuals and, when reconstructed, show no differences from the holotype. They were all collected at the same horizon within a few metres of each other and within a few tens of metres from the holotype. In addition, a partial rostrum and partial mandible are known from the Fish Bed horizon of the Kulu Formation (c. 17 M.y.) at Nyamuga, Rusinga Island, Kenya. This specimen also seems to be referable to *C. pigotti*, although the external nares are of about equal length and width and the teeth are longer and narrower than in the holotype.

The small size of the holotype and the referred individuals is probably real rather than due to immaturity. The following features seen in the skull of *C. pigotti* are characteristic of adult crocodiles according to Joffe's (1967) criteria: the skull is well ossified and rugose; the sutures on the dorsal surface of the skull are obscure; the

TABLE 2. Proportional indices for three related species.

*Indices\**

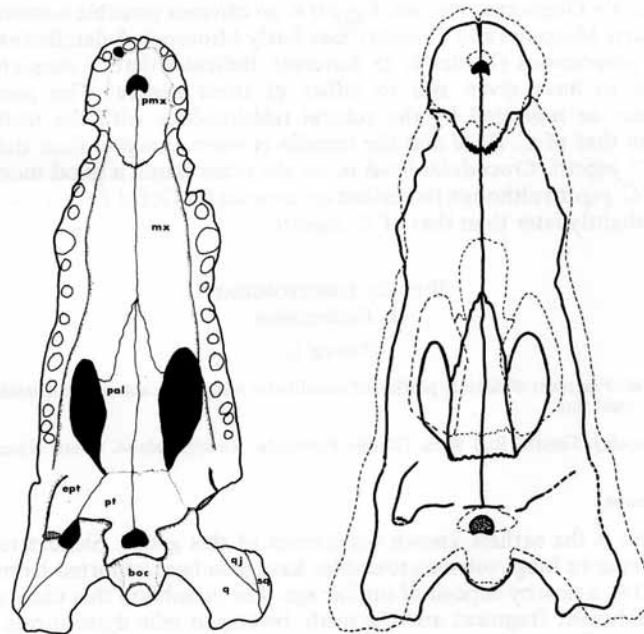
1.  $\frac{\text{Width of skull (across anterior ends of orbits)}}{\text{Width of skull (across quadratojugals)}}$
2.  $\frac{\text{Width of skull (across 5th maxillary tooth)}}{\text{Width of skull (across quadratojugals)}}$
3.  $\frac{\text{Length of premaxilla (along the ventral median suture)}}{\text{Distance along premaxillae-maxillae suture to middle of 9th max. tooth}}$
4.  $\frac{\text{Height of skull}}{\text{Length of skull (occipital condyle to tip of snout)}}$
5.  $\frac{\text{Width of skull (across quadratojugals)}}{\text{Length of skull (supraoccipital to tip of snout)}}$
6.  $\frac{\text{Width of skull (across premaxillae)}}{\text{Width of skull (across anterior ends of orbits)}}$
7.  $\frac{\text{Width of skull (across premaxillae)}}{\text{Width of skull (across anterior end of palatines)}}$
8.  $\frac{\text{Width of skull (across premaxillae)}}{\text{Height of skull (base of pterygoid to top of supraoccipital)}}$
9.  $\frac{\text{Height of skull (base of pterygoid to top of supraoccipital)}}{\text{Width of skull (across 5th maxillary tooth)}}$
10.  $\frac{\text{Width of skull (across premaxillae)}}{\text{Length of premaxilla (along the ventral median suture)}}$
11.  $\frac{\text{Width of skull (across 5th maxillary tooth)}}{\text{Distance along premaxillae-maxillae suture to middle of 9th max. tooth}}$

	<i>C. lloidi</i> (Plio-Pleistocene, East Africa)			<i>C. niloticus</i> (Recent, Lake Rudolf)			<i>C. pigotti</i> (Early Miocene, East Africa)
	range	mean	N	range	mean	N	
1.	0.65-0.84	0.77	8	0.67-0.77	0.70	18	0.77
2.	0.49-0.70	0.64	6	0.51-0.63	0.55	14	0.66
3.	0.50-0.52	—	2	0.51-0.61	0.55	32	0.61
4.	0.21-0.28	0.25	7	0.17-0.21	0.19	21	0.17
5.	0.63-0.70	0.66	6	0.45-0.56	0.50	13	0.46
6.	0.44-0.66	0.53	6	0.41-0.50	0.44	35	0.41
7.	0.57-0.71	0.64	12	0.54-0.70	0.63	42	0.54
8.	0.73-1.12	0.97	5	0.48-0.71	0.64	14	0.87
9.	0.58-0.88	0.66	5	0.58-0.99	0.87	17	0.55
10.	1.04-1.53	1.31	9	0.64-0.82	0.75	41	0.67
11.	0.83-1.37	1.09	9	0.59-0.90	0.71	32	0.84

\* The indices represented here show the proportions of the skull in which *C. pigotti* differs from *C. lloidi* and *C. niloticus*.

TABLE 3. Skull measurements of *C. pigotti* (in mm).

Length of skull (occipital condyle to tip of snout)	337	Length of external nasal aperture	24
Length of skull (supraoccipital to tip of snout)	337	Width of external nasal aperture	24
Tip of snout to extremities of quadratojugal	362	Length of palatine fenestra	75
Height of skull (base of pterygoid to top of supraoccipital)	57	Inter-palatine fenestral constriction (minimal size)	34
Width of skull (across quadratojugals)	56	Width of palatine fenestra	26
Width of skull (across anterior ends of orbits)	121	Length of premaxilla (along the ventral median suture)	75
Width of skull (across postorbital column)	135	Length of maxilla (along the ventral median suture)	82
Width of skull (across premaxillae) (Minimal)	50	Length of palatine (along the ventral median suture)	101
Maximal width of premaxillae	63	Length of pterygoids (along the ventral median suture, to posterior end of internal narial aperture)	48
Width of skull (across 5th maxillary tooth) (Maximal)	103	Distance between premaxillary suture to middle of 9th maxillary tooth	123
Width of skull (across anterior ends of palatines)	92		
Length of snout (anterior end of orbit to tip of snout)	232		
Length of orbit	37		
Width of orbit	30		
Interorbital constriction (minimal width)	26		



TEXT-FIG. 1. Left, ventral outline drawing of *Crocodylus pigotti* to show sutural and fenestral relationships. Scale as in Plate 99. Right, ventral outline of *C. niloticus* (outer broken line) superimposed on ventral outline of *C. pigotti* (inner continuous line) to show differences in proportions.

supratemporal fenestrae are nearly circular, and the snout is relatively long compared to the postorbital length (this last is a phylogenetic as well as ontogenetic feature, however). This species may be represented by larger individuals in the Gumba Red Beds of Rusinga Island and perhaps elsewhere in the Early Miocene of East Africa, but the remains are too fragmentary to be certain. The mean body size of *C. niloticus* varies today in different basins: those from Aswa River in northern Uganda and Lake Baringo, for example, are much smaller than those from the Nile (Cott 1961).

*Relationships.* The general proportions of *C. pigotti* are similar to those of *C. niloticus*. Basic differences occur, however, in the location of some skull structures, particularly in the position of the palatal sutures in relation to the maxillary tooth row as described above. This similarity in proportions, combined with a different organization of skull elements, demonstrates that *C. pigotti* is a species that evolved earlier than *C. niloticus* but in parallel with it to fill a similar ecological zone. The measured parameters are given in Table 3.

Rostral elongation is a common evolutionary phenomenon in crocodiles although the reverse has not occurred (Tchernov 1976). Thus, *C. megarhinus*, which is the only brevirostrine *Crocodylus* known from the pre-Miocene record of Africa (?Late Eocene or ?Early Oligocene, Fayum, Egypt) is an obvious possible ancestor for both *C. pigotti* (Early Miocene) and *C. lloidi* (?late Early Miocene). A detailed examination of the skull proportions (Tables 1, 2), however, indicates that *C. megarhinus* is too long-snouted to have given rise to either of these genera. The premaxilla of *C. megarhinus*, as indicated by the sutural relationships with the teeth, is more elongate than that of *C. lloidi* and the maxilla is more elongate than that of either *C. lloidi* or *C. pigotti*. *Crocodylus lloidi* is, on the other hand, a good morphological ancestor for *C. pigotti* although its earliest occurrence (at Gebel Zelten and Moghara) is probably slightly later than that of *C. pigotti*.

?Family TOMISTOMIDAE

cf. *Euthecodon*

(Text-fig. 2)

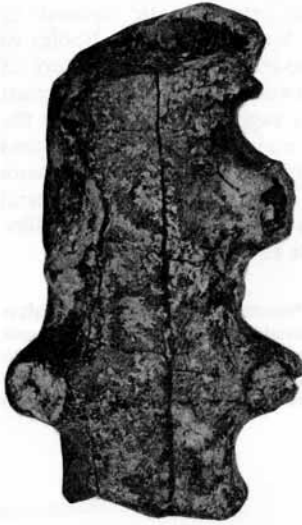
*Referred Material.* Fragment of dentary portion of mandibular symphysis, anterior to splenial (KNM-RU 2585, Field No. 1808 '50).

*Horizon and Locality.* Gumba Red Beds, Gumba Peninsula, Rusinga Island, South Nyanza Province, Kenya.

*Age.* Early Miocene.

*Remarks.* This is the earliest known occurrence of this genus. Slender teeth of the type which occur in longirostrine crocodiles have also been reported from Karungu (Andrews 1914), a nearby deposit of similar age. The possibility that these specimens, both the mandibular fragment and the teeth, belong to relic dyrosaurids should be kept in mind, although the angle with which the sockets meet the ramus and the spacing of the sockets are identical with those of *Euthecodon*.





TEXT-FIG. 2. Fragment of dentary of cf. *Euthecodon* (KNM-RU 2585) from the Gumba Red Beds, Gumba Peninsula, Rusinga Island, Kenya.  $\times 1.2$ .

#### DISCUSSION

In the Paleogene, *Crocodylus* and *Tomistoma* flourished along the southern shore of the Tethys (Andrews 1905, 1906; Müller 1927), but have not been found at other crocodile-bearing localities of similar age in West Africa (cf. Signeux 1968). Their descendants are found in equatorial Africa (*C. lloidi*, *C. pigotti*, *Euthecodon*) in the Early Miocene in deposits formed by rivers draining westwards to the Congo Basin (cf. Andrews and Van Couvering 1975). How did they get there? Geomorphological (Butzer and Hansen 1968) and sedimentological data (Hassan 1976) indicate that the Nile drainage did not connect with equatorial Africa until Early Pleistocene or later. Either these crocodiles migrated along the western coast of Africa leaving no known fossil record, or intermittent drainage connections allowed them to migrate southward from the Tethyan coast. The absence of Tertiary deposits over most of Africa makes any conclusions extremely tenuous.

*Crocodylus pigotti* is widespread ecologically in Early Miocene deposits. The specimens which have definitely been referred to this species occur in both lake floor and riverine flood basin deposits, implying that this crocodile was equally at home in lakes and rivers. The specimens from the lake deposits are in general noticeably smaller than those from the flood basin deposits.

*Euthecodon* occurs in the Gumba Red Beds of Rusinga Island, together with jaw and tooth fragments of a crocodile similar to *C. niloticus*, possibly *C. pigotti* but about half as large again. These deposits are highly oxidized, fine-grained, riverine flood basin deposits. *Lates*, the 'Nile' perch, *Polypterus*, the bichir, *Protopterus*, the

African lungfish, and *Etheria*, a fresh-water 'oyster', are other aquatic elements of the fauna. *Lates* requires well-oxygenated (Fish 1956), large, permanent bodies of water, while *Polypterus* and *Protopterus* can live in poorly oxygenated waters as well. *Etheria* is reported by Sandford (1936) to occur in swamps, although Verdcourt (1963) states that it is found in large rivers or lakes. We suggest, therefore, that the Gumba Red Beds were deposited in the flood basin of a major river. *Euthecodon* and *Crocodylus* (?*C. pigotti*) co-existed in this river, the former as an aquatic piscivore and the latter as a semi-aquatic carnivore preying on both aquatic and terrestrial animals. This aquatic fauna, excluding *Euthecodon*, can be found today in the Nilo-Sudan and Zaïrean ichthyofaunal provinces (cf. Roberts 1975).

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