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THE OSTEOLOGY AND RELATIONSHIPS OF  
*TANGASAUROS MENNELLI* HAUGHTON  
(REPTILIA, EOSUCHIA)

By

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By

PHILIP J. CURRIE

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(With 6 figures and 2 tables)

[MS accepted 11 November 1981]

ABSTRACT

The osteology of *Tangasaurus mennelli*, an eosuchian reptile from the Upper Permian of Tanzania, reveals a number of adaptations for an aquatic existence. Specimens from Madagascar that were attributed to *Tangasaurus mennelli* represent a distinct, as yet unnamed, genus that is related to *Tangasaurus* but less specialized. *Tangasaurus* is closely related to, but less specialized for an aquatic life than *Hovasaurus boulei* of the Upper Permian of Madagascar. The taxonomy of younginids and tangasaurids is re-examined, and it is concluded that these families together comprise a distinct taxonomic unit, the Younginoidea, that did not give rise to any other eosuchians.

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INTRODUCTION

Eosuchians are generally considered to be the basal stock from which all later diapsids evolved. Recent papers by Carroll (1975, 1976a, 1976b, 1977, 1978), Currie (1980, 1981), Gow (1975), Harris & Carroll (1977), and Reisz (1977) have shown that eosuchians originated earlier and were more diverse than previously suspected. By the end of the Permian, at least three distinct lines had developed. One line is characterized by cervical elongation as in *Prolacerta* (Gow 1975) and the highly specialized *Tanystropheus* (Wild 1973). A separate lineage of eosuchians might have given rise to lizards (Carroll 1975) and the

gliding genus *Daedalosaurus* (Carroll 1978). *Youngina* is one of a diverse assemblage of terrestrial and aquatic forms that appears to have given rise to archosaurs (Carroll 1976a) and sauropterygians (Carroll 1981). The more detailed relationships of some of these taxa are considered here.

Four genera of reptiles seem to share a common ancestry with *Youngina*: *Tangasaurus* (Haughton 1924), a Late Permian reptile specialized for an aquatic existence, known from Tanzania; *Kenyasaurus* (Harris & Carroll 1977), a terrestrial relative of *Tangasaurus* from Lower Triassic strata of Kenya; and '*Datheosaurus*'\* and *Hovasaurus* from Upper Permian beds of Madagascar. '*Datheosaurus*' was a terrestrial form like *Kenyasaurus*, whereas *Hovasaurus* was even more specialized for an aquatic existence than was *Tangasaurus*. Descriptions have recently been published on *Youngina* (Gow 1975) and *Kenyasaurus* (Harris & Carroll 1977), and papers on '*Datheosaurus*' and *Hovasaurus* are being prepared by Carroll and Currie respectively. The purpose of this paper is to redescribe the known specimens of *Tangasaurus* and to compare them with other tangasaurids.

In 1924 S. H. Haughton described two fossil reptile specimens that had been collected from Upper Permian strata in the vicinity of Tanga, in what is now Tanzania. These were recognized as a previously unknown taxon and named *Tangasaurus mennelli*. Although the specimens were designated as co-types, the smaller, better preserved one (Fig. 1A) is here considered as the lectotype. It is in the museum in Bulawayo, Zimbabwe, while its counterpart, SAM-6231 (Fig. 1B), and the larger specimen, SAM-6232 (Fig. 1C), are in the South African Museum, Cape Town. On the basis of postcranial characteristics, Haughton (1924) felt that *Tangasaurus* was probably a diapsid reptile that, because of the long, powerful, flattened tail, had become adapted for an aquatic existence.

Numerous specimens of small reptiles had been collected in beds of approximately the same age along the Sakamena River of southern Madagascar. One of the animals collected was described as *Broomia madagascariensis* (Piveteau 1925), but was referred the following year by Piveteau to *Tangasaurus menelli* (*sic*). Contrary to Haughton, Piveteau felt that *Tangasaurus* was a primarily terrestrial animal. Following Nopcsa (1924), he considered it to be related to *Araeoscelis*, *Kadliosaurus*, *Broomia*, *Saurosternon*, and *Pleurosaurus*.

A new genus and species, *Hovasaurus boulei*, also from Madagascar, described by Piveteau (1926) was considered to be related to *Mesosaurus*. Although not as specialized as *Mesosaurus* for living in the water, Piveteau felt that the short neck, short manus, well developed haemal spines and slight pachyostosis of the ribs showed that *Hovasaurus* was an aquatic animal.

Haughton (1930) restudied Piveteau's specimens from Madagascar, concluding that *Tangasaurus* and *Hovasaurus* were allied and that both were diapsids. *Hovasaurus* was recognized as a reptile adapted to an aquatic existence through reduction of the forelimb and coracoid, and retarded ossification and

\* While this paper was in press '*Datheosaurus*' specimens were redescribed as *Thadeosaurus* (Carroll 1981).

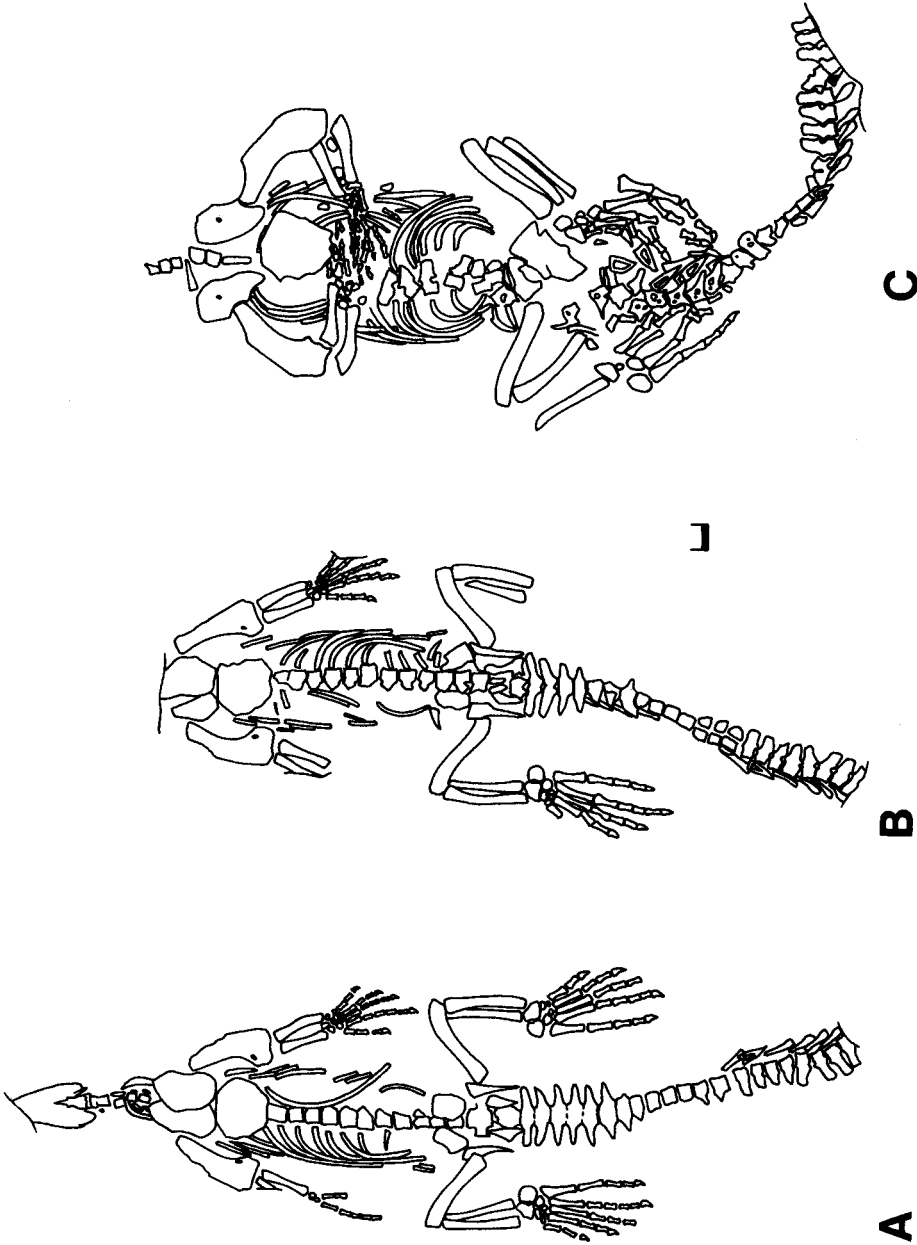


Fig. 1. *Tangasaurus mennelli*. A. Ventral view of lectotype in Bulawayo Museum, Zimbabwe. B. SAM-6231, counterpart of preceding specimen (from Harris & Carroll 1977). C. SAM-6232, ventral view. Scale = 1 cm.

elongation of the body. *Tangasaurus* was considered to be morphologically intermediate between *Youngina* and *Hovasaurus*.

Other specimens described by Piveteau (1926) were not associated with *Tangasaurus* and *Hovasaurus* until recently. A large number of caudal sections were recovered along the Sakamena River of Madagascar. The caudal vertebrae have high neural spines, and the haemal spines are long and plate-like. Piveteau recognized these as belonging to a reptile adapted to swimming, but did not have any other skeletal elements associated with the caudal vertebrae. These are now known to belong to *Hovasaurus*.

A third genus recognized by Piveteau (1926: 171–172) was assigned with doubt to the European genus *Datheosaurus*, now considered to be congeneric with *Haptodus* (Currie 1979), a sphenacodont pelycosaur. The specimens referred to this genus were restudied recently by Carroll (1981) who considers them to be a new genus. Morphologically this animal appears to be close to the ancestral stock of *Tangasaurus* and *Hovasaurus*.

*Kenyasaurus mariakeniensis* from the Lower Triassic of Kenya (Harris & Carroll 1977) is considered to be most closely comparable with *Tangasaurus* and *Hovasaurus* on the basis of general body form, the presence of a sternum and, particularly, the anatomy of the foot.

Piveteau (1926) included *Broomia*, *Saurosternon* and *Tangasaurus* in the Tangasaurinae (*sic*). After Haughton's paper of 1930 demonstrated the anatomical similarities between *Tangasaurus* and *Hovasaurus*, these genera were usually included as the only representatives of the family Tangasauridae (Camp 1945; Romer 1956, 1966; Piveteau 1955; Orlov 1964; Kuhn 1969). Depending on how the various authors have classified primitive diapsid reptiles, the Tangasauridae have been referred to the Araeosceloidea (Nopcsa 1924; Piveteau 1926), Eosuchia (Haughton 1930; Von Huene 1940, 1952; Piveteau 1955; Romer 1956, 1966; Kuhn 1969), Prolacertilia (Watson 1957; Orlov 1964) or Protorosauria (Camp 1945).

In re-examining the anatomy of tangasaurids, it became obvious that there is a great deal of confusion concerning the identification and anatomy of these animals. The anatomy of *Tangasaurus* and *Hovasaurus* is very similar, and there are few characters to distinguish these genera. Although more than 300 tangasaurid specimens were collected in Madagascar, in almost every case two of the most diagnostic parts of the body—the skull and the tail—were missing. The problem is compounded by poor preservation of the type specimens of *Tangasaurus mennelli* from Tanzania that generally have been ignored in favour of the better preserved specimens from Madagascar. Finally, many of the specimens have been misidentified because they are immature and show few distinctive characters. As part of a revision of tangasaurid anatomy, the majority of specimens that have been figured were re-examined and, in many cases, re-identified (Table 1). Hopefully, the confusion concerning the identification of tangasaurids has been resolved. This will permit more accurate conclusions concerning evolutionary and developmental lineages, palaeoecology, geographic

TABLE 1  
Figured specimens of Tangosauridae.

Identification (this paper)	Specimen number	Previous identification
' <i>Datheosaurus</i> '	MNHN 1908-5-1	<i>Tangasaurus mennelli</i> (Piveteau 1926, pl. 12 (fig. 1))
' <i>Datheosaurus</i> '	MNHN 1908-11-4	<i>T. mennelli</i> (Piveteau 1926, pl. 10 (fig. 2))
' <i>Datheosaurus</i> '	MNHN 1908-11-5	<i>T. mennelli</i> (Piveteau 1926, pl. 11 (fig. 2), text-figs 17-18; Piveteau 1955, fig. 9; Gladstone & Wakeley 1932 fig. 2; Kuhn 1969, figs 18-6, 18-8)
' <i>Datheosaurus</i> '	MNHN 1908-11-6	<i>T. mennelli</i> (Piveteau 1926, pl. 16 (fig. 2))
' <i>Datheosaurus</i> '	MNHN 1908-11-7	<i>T. mennelli</i> (Piveteau 1926, pl. 10 (fig. 1))
' <i>Datheosaurus</i> '	MNHN 1908-11-19	? <i>Datheosaurus</i> sp. (Piveteau 1926, pl. 17 (fig. 2))
<i>Hovasaurus boulei</i>	MNHN 1908-21-2	<i>Hovasaurus boulei</i> (Piveteau 1926, pl. 8 (fig. 2))
<i>H. boulei</i>	MNHN 1908-21-7	<i>H. boulei</i> (Piveteau 1926, pl. 8 (fig. 1); Haughton 1930, fig. 3C)
<i>H. boulei</i>	MNHN 1908-21-8	<i>H. boulei</i> (Piveteau 1926, pl. 7 (fig. 1))
<i>H. boulei</i>	MNHN 1908-21-10	<i>T. mennelli</i> (Harris & Carroll 1977, text-fig. 5B)
<i>H. boulei</i>	MNHN 1908-21-11	Indeterminate reptile (Piveteau 1926, pl. 10 (fig. 4))
<i>H. boulei</i>	MNHN 1908-21-16	<i>T. mennelli</i> (Piveteau 1926, pl. 15 (fig. 5) text-fig. 20; Gladstone & Wakeley 1932, text-fig. 2)
<i>H. boulei</i>	MNHN 1908-32-22	<i>H. boulei</i> (Piveteau 1926, pl. 9 (fig. 4), text-fig. 14)
<i>H. boulei</i>	MNHN 1908-32-23	<i>H. boulei</i> (Piveteau 1926, pl. 9 (figs 1-2, text-fig. 16))
<i>H. boulei</i>	MNHN 1908-32-24	<i>T. mennelli</i> (Piveteau 1926, pl. 13 (fig. 1); Harris & Carroll 1977, text-fig. 5A)
<i>H. boulei</i>	MNHN 1908-32-25	<i>T. mennelli</i> (Piveteau 1926, pl. 14 (fig. 3))
<i>H. boulei</i>	MNHN 1908-32-26	<i>T. mennelli</i> (Piveteau 1926, pl. 15 (fig. 1))
<i>H. boulei</i>	MNHN 1908-32-29	<i>H. boulei</i> (Piveteau 1926, pl. 7 (fig. 2))
<i>H. boulei</i>	MNHN 1925-5-30	<i>H. boulei</i> (Piveteau 1926, pl. 9 (fig. 3), text-fig. 12)
<i>H. boulei</i>	MNHN 1925-5-31	<i>T. mennelli</i> (Piveteau 1926, pl. 15 (fig. 4), text-fig. 22; Piveteau 1955, text-fig. 10)
<i>H. boulei</i>	MNHN 1925-5-32	<i>T. mennelli</i> (Piveteau 1926, pl. 16 (fig. 1), text-fig. 23; Haughton 1930, text-fig. 4C; Piveteau 1955, text-fig. 11; Kuhn 1969, text-fig. 18-7; Harris & Carroll 1977, text-fig. 5C)
<i>H. boulei</i>	MNHN 1925-5-33	<i>T. mennelli</i> (Piveteau 1926, pl. 10 (fig. 3))
<i>H. boulei</i>	MNHN 1925-5-34	<i>T. mennelli</i> (Piveteau 1926, pl. 14 (fig. 2); Camp 1945, text-fig. 10)
<i>H. boulei</i>	MNHN, number unknown	<i>H. boulei</i> (Piveteau 1926, pl. 7 (fig. 3); Haughton 1930, text-fig. 1A)
? <i>H. boulei</i>	MNHN, number unknown	<i>T. mennelli</i> (Piveteau 1926, pl. 13 (fig. 5), pl. 14, fig. 1)
<i>Kenyasaurus mariakaniensis</i>	KNM-MA1	<i>Kenyasaurus mariakaniensis</i> (Harris & Carroll 1977, text-figs 1-4)
<i>Tangasaurus mennelli</i>	SAM-6231	<i>Tangasaurus mennelli</i> (Haughton 1924, pl. 2, text-figs 1-3; Von Huene 1926, text-fig. 33; Romer 1956, text-fig. 186E; Orlov 1964, text-fig. 468; Kuhn 1969, text-figs 17-12; Harris & Carroll 1977, text-fig. 6)
<i>T. mennelli</i>	SAM-6232	<i>T. mennelli</i> (Haughton 1924, pl. 1)
Not a tangasaurid	MNHN 1909-3-30	<i>T. mennelli</i> (Piveteau 1926, pl. 15 (figs 2-3))
Not a tangasaurid	MNHN, number unknown	<i>T. mennelli</i> (Piveteau 1926, pl. 13 (figs 2, 2A))
Not a tangasaurid	MNHN, number unknown	<i>T. mennelli</i> (Piveteau 1926, pl. 13 (fig. 3))
Not a tangasaurid	MNHN, number unknown	<i>T. mennelli</i> (Piveteau 1926, pl. 13 (figs 4, 4A))

distribution and stratigraphy. One unfortunate result is that *Tangasaurus* can no longer be used for biostratigraphic correlation of the middle division of the Tanga beds of Tanzania with the Lower Sakamena Formation of Madagascar (McKinlay 1956, 1960).

Tangasaurid eosuchians were relatively small lizard-like reptiles. The largest is *Hovasaurus* with an estimated maximum snout-vent length of about 30 cm. The largest specimen of *Tangasaurus* is 20 per cent smaller than the largest *Hovasaurus*, but it can be inferred from the incompleteness of ossification that larger specimens probably existed. The linear dimension of a mature specimen of '*Datheosaurus*' are about 35 per cent smaller than the same dimensions in *Hovasaurus*. Proportions and lengths listed in this paper for *Hovasaurus* and '*Datheosaurus*' were estimated for adult size from the allometric growth curves.

*Hovasaurus* and *Kenyasaurus* are valid genera. Use of the name *Tangasaurus* in this paper is restricted to the two specimens from Tanzania. When referring to generic characters attributed by Piveteau (1926), Houghton (1930), and others to specimens from both Tanzania and Madagascar, the name *Tangasaurus* will be used in quotation. '*Datheosaurus*' is used to refer to most of the specimens from Madagascar that Piveteau (1926) identified as *Datheosaurus* and *Tangasaurus*.

The following abbreviations have been used when giving specimen numbers:

MNHN, Muséum National d'Histoire Naturelle  
SAM, South African Museum

## DESCRIPTION

### SKULL

Cranial anatomy is poorly known in tangasaurids. In one of the two known specimens of *Tangasaurus*, the poorly preserved skull is exposed in palatal aspect. The bone is crushed flat, and seems little better than a film of carbon. Further preparation of the specimen seems unfeasible. The anterior portion of the skull was not collected, but the preserved portion is 38 mm in length. Houghton (1924) felt that the full length of the skull would have been between 50 and 60 mm. In the light of the anterior tapering of the skull, there was probably no elongate snout, and it is doubtful that the skull would have exceeded 45 mm. The only bone that can be identified with any degree of certainty is the basisphenoid-parasphenoid complex. The cultriform process is long and tapering, and the basipterygoid processes appear to be short. The complex is concave ventrally in transverse section between the tuberosities. Houghton (1924) made observations on the pterygoid and various palatal vacuities, but none of these can be seen clearly enough in the specimen to merit description. The basioccipital can be seen at the back of the skull, but shows no distinctive characters. Von Huene (1926) identified one bone as either stapes or



quadrate, but whatever it is, the bone gives us no better understanding of the skull.

Only the postorbital and palatal regions of the skull of *Hovasaurus* are known. The contours and proportions of the parasphenoid-basisphenoid complex of *Tangasaurus* are similar to those of *Hovasaurus*.

#### VERTEBRAE AND RIBS

Haughton (1924) estimated that there were eighteen presacral vertebrae in the lectotype (SAM-6231) of *Tangasaurus mennelli*. This number is much less than that of other eosuchians, and it is assumed that he had not included the cervical vertebrae in his total. Because he stated that there were seven or fewer anterior vertebrae obscured by bones of the pectoral girdle, his estimated presacral count can be raised to a maximum of twenty-five. This is the number of vertebrae found in *Hovasaurus*. As in *Hovasaurus*, the neck of *Tangasaurus* is short—probably including only five vertebrae.

Primitive diapsid reptiles characteristically have two sacral vertebrae. Haughton (1924: 3) stated that one specimen of *Tangasaurus mennelli* (SAM-6231) had three fused sacral vertebrae. However, preservation in the sacral region of this specimen is poor, and it is likely that he misinterpreted the first caudal rib as a sacral rib. In a later paper Haughton (1930) stated that '*Tangasaurus*' has two sacrals.

The total length of the tail is known in few eosuchians. 24 caudal vertebrae are preserved in the lectotype of *Tangasaurus*, and 28 in SAM-6232. However, the tail was clearly much longer than this. '*Datheosaurus*' has at least 45 caudals and *Hovasaurus* probably had more than 70.

Details of the dorsal vertebrae are difficult to delineate in the type specimens of *Tangasaurus*. In *Hovasaurus*, there is a process at the base of the neural spine that acts as an extra intervertebral articulation (Fig. 2). A similar accessory process appears to be present in at least one of the dorsal vertebrae of the larger specimen of *Tangasaurus*. Contact between the neural spines has also been noted in *Youngina* (Currie 1981), '*Datheosaurus*', and *Kenyasaurus*.

Specimens of *Tangasaurus* (Figs 3A–B, 4) have caudal vertebrae that are specialized for propulsion in water. The neural spines are high and the haemal spines are long and expanded distally. The neural spines of the mid-caudals are higher than the presacral neural spines, but are not as long as the haemal spines. The specialization is not as great as in *Hovasaurus* (Fig. 3D) in that the neural spines are relatively lower, only about 35 per cent greater than the length of the associated centrum compared with more than 125 per cent in *Hovasaurus*. Nevertheless, the caudal specialization suggests that *Tangasaurus* and *Hovasaurus* are closely related. Specimens from Madagascar attributed to '*Tangasaurus*' and '*Datheosaurus*' have unspecialized caudal vertebrae with low neural spines (Fig. 3C).

The dorsal ribs of *Tangasaurus* have a single head and are not pachyostotic.

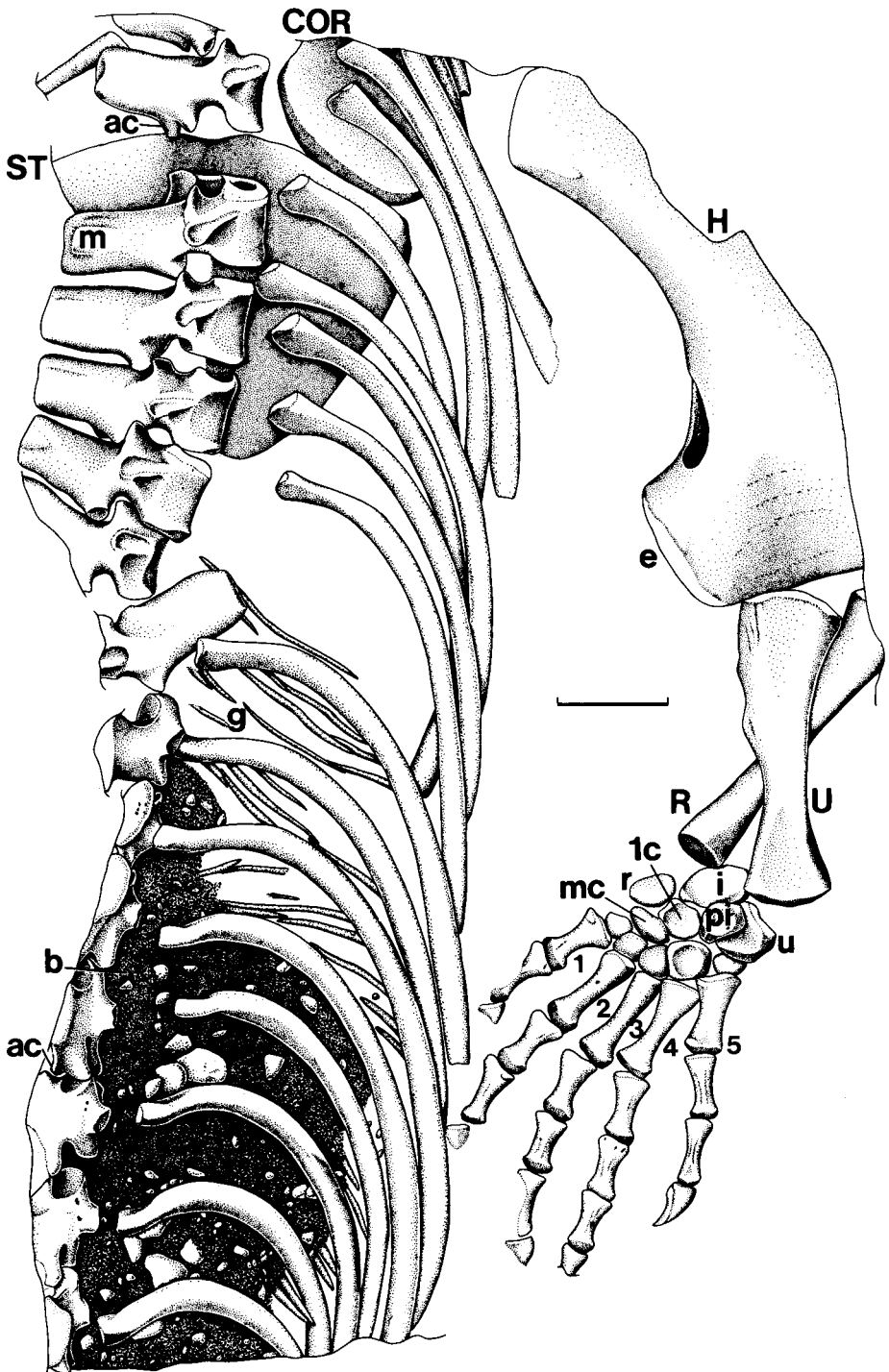


Fig. 2. *Hovasaurus boulei*, MNHN 1908-32-59. Abbreviations: ac—accessory articulation on neural spine, b—ballast, COR—coracoid, e—entepicondyle, g—gastralia, H—humerus, i—intermedium, lc—lateral centrale, m—mammillary process, mc—medical centrale, pi—pisiform, R—radius, r—radiale, ST—sternum, U—ulna, u—ulnare. Scale = 1 cm.

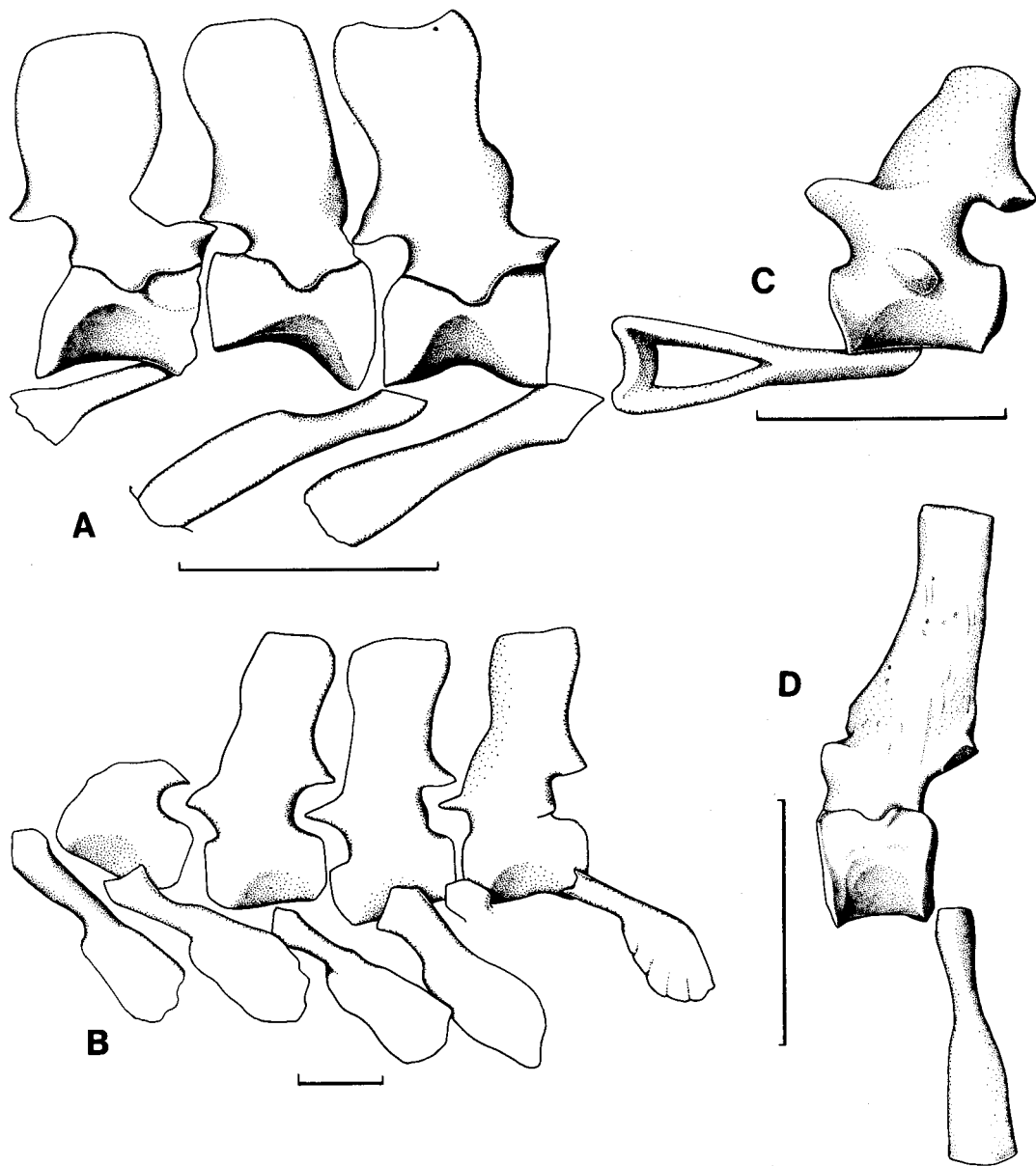


Fig. 3. Caudal vertebrae of tangasaurid eosuchians. A. *Tangasaurus* (Bulawayo Museum), 19th to 21st, right aspect. B. *Tangasaurus*, SAM-6232, 20th to 23rd, left view. C. '*Datheosaurus*', MNHN 1908-5-1, mid-caudal, left view. D. *Hovasaurus*, MNHN 1908-32-64, 14th caudal, left aspect. Each scale = 1 cm.

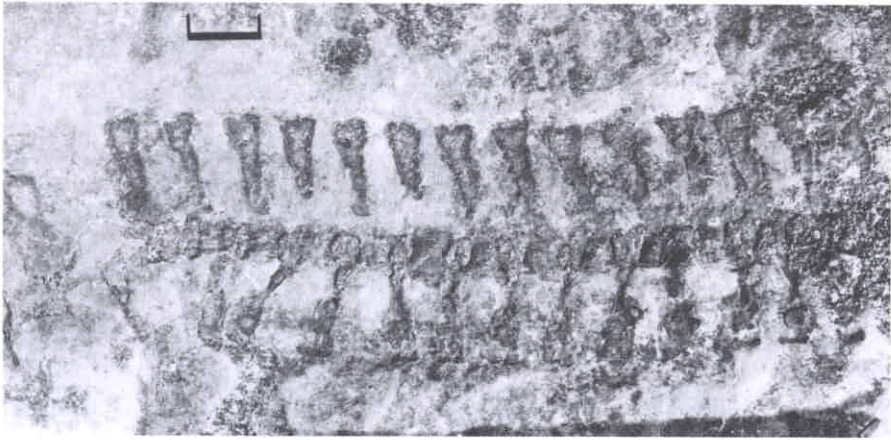


Fig. 4. *Tangasaurus mennelli*, SAM-6233, caudal vertebrae. Scale = 1 cm.

In *Hovasaurus*, moderate pachyostosis can be seen in the ribs of large individuals but it is usually not apparent in juveniles.

An exact count of caudal ribs is not possible because of the poor preservation of the *Tangasaurus* specimens. The total number, however, would have been between 9 and 12. There are a maximum of 12 pairs of caudal ribs in *Hovasaurus* and an additional 2 pairs of transverse processes. Nineteen pairs of caudal ribs and transverse processes are found in specimens from Madagascar that were formerly attributed to *Tangasaurus*, and 28 pairs in *Kenyasaurus*.

#### APPENDICULAR SKELETON

Both Piveteau (1926) and Haughton (1924, 1930) recognized that the relative lengths of elements of the appendicular skeleton change with age. More precise calculations (Currie in preparation) have shown that '*Tangasaurus*' specimens of Madagascar are juveniles of '*Datheosaurus*', and that the allometric growth coefficients for '*Datheosaurus*' and *Hovasaurus* are different (Fig. 5).

The two specimens of *Tangasaurus* represent animals of different ages and consequently show some differences in limb proportions. Comparison can be made with *Hovasaurus* by means of the allometric growth equations. The constants  $b'$  and  $k_{yx}$  power equation  $y = b'x^{k_{yx}}$  (Currie 1978) were solved to describe a growth series of *Hovasaurus boulei*. The average length of a dorsal centrum that serves as the base for comparison is represented by  $x$ , while the length of the element being compared is represented by  $y$ . From this information, the expected mean length (in millimetres) of each element was computed for *Hovasaurus* specimens of the same size as the *Tangasaurus* specimens SAM-6231 ( $x = 6,6$  mm) and SAM-6232 ( $x = 8,0$  mm). Lengths of the metacarpals and metatarsals were not included in the lengths of the digits of the manus and

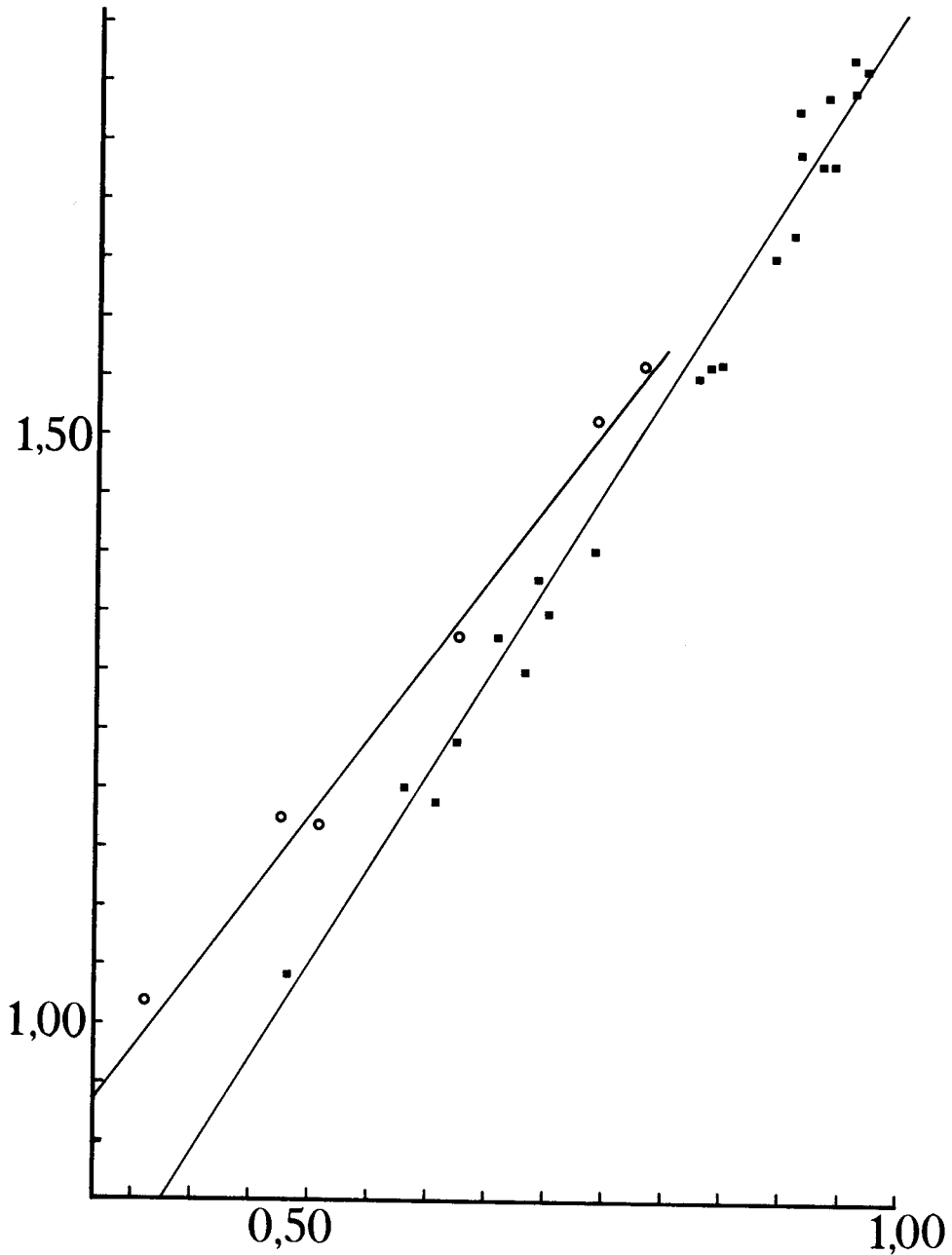


Fig. 5. Relationship between humerus length (ordinate) and length of associated thoracic centrum (abscissa) in '*Datheosaurus*' (circles) and '*Hovasaurus*' (squares). Measurements converted to logarithms and plotted on arithmetic paper. Differences in slope represent differences in allometric growth coefficients.

pes. With the exception of the length of metatarsal IV of SAM-6231 and the length of digit IV of the pes of SAM-6232, all measurements fell within the 95 per cent confidence intervals for these dimensions in *Hovasaurus* (Table 2). This shows that the relative lengths of limb elements are almost the same in *Tangasaurus* and *Hovasaurus*, which also suggests close relationship because of the specialized proportions of *Hovasaurus* limbs for swimming.

In the smaller specimen of *Tangasaurus* (SAM-6231), the humerus is shorter than the femur, whereas the femur is the shorter of the two in the larger specimen. This suggests that the humerus grew faster than the femur as the animal increased in size. The same thing happens in both '*Datheosaurus*' and *Hovasaurus* where more complete growth series are known. Haughton (1930) stated that the limbs of '*Tangasaurus*' are longer relative to the body than those of *Hovasaurus*. However, it is now known that the humerus of *Tangasaurus* is 5,8 times the length of a dorsal centrum ( $\bar{x}$ ), that of a mature '*Datheosaurus*' is 6,7 $\bar{x}$ , and that of a mature specimen of *Hovasaurus* is 7,1 $\bar{x}$ . Similarly, other limb elements of *Tangasaurus* have slightly smaller relative lengths than the same elements in *Hovasaurus*.

In *Tangasaurus*, the radius is 60 per cent the length of the humerus,

TABLE 2

Comparisons of the lengths of postcranial elements of *Hovasaurus boulei* and *Tangasaurus mennelli*. The constants  $b'$  and  $k_{yx}'$  of the power equation  $y = b'x^{k_{yx}'}$  have been solved to describe growth series of *H. boulei*. From this information, the expected mean lengths (in mm) of each element have been computed for *H. boulei* specimens the same size as the co-types of *T. mennelli* ( $x = 6,6$  mm for SAM-6231, 8,0 mm for SAM-6232). Lengths of the metacarpals and metatarsals are not included in the lengths of the digits of the manus and pes. Abbreviations: N—size of sample, R—correlation coefficient.

$y =$ length of	N	R	$k_{yx}'$	$b'$	$x$	Estimated mean value of $y$ for <i>H. boulei</i>	Measured value of $y$ for <i>T. mennelli</i>
						95% confidence interval	
Coracoid	9	0,981	2,229	0,360	6,6	24,1	25,3
					8,0	37,0	31,7
Sternum	15	0,987	1,780	0,739	6,6	22,1	21,8
					8,0	29,9	30,3
Humerus	20	0,993	1,638	1,674	6,6	36,8	36,0
					8,0	50,5	48,5
Radius	13	0,994	1,306	1,893	6,6	22,2	21,6
					8,0	28,6	28,0
Metacarpal IV	12	0,991	1,354	0,599	6,6	7,7	8,0
Digit IV (manus)	12	0,983	1,236	2,035	6,6	20,9	21,0
Ilium	14	0,996	1,067	2,952	6,6	22,1	23,0
Femur	16	0,990	1,334	3,146	6,6	39,0	39,0
					8,0	50,4	47,2
Tibia	15	0,991	1,298	2,872	6,6	33,2	34,0
					8,0	42,6	40,0
Metatarsal IV	14	0,995	1,340	1,310	6,6	16,4	17,4
					8,0	21,2	20,5
Digit IV (Pes)	9	0,991	1,493	1,996	6,6	33,3	32,2
					8,0	44,5	39,1

whereas in mature *Hovasaurus* it is only 52 per cent. In the relatively unspecialized '*Datheosaurus*' the radius is 54 per cent the length of the humerus at maturity. Relative to the length of a dorsal centrum, however, the length of the forearm of *Tangasaurus* is only 3,3x, whereas that of *Hovasaurus* is the same as '*Datheosaurus*' (3,7x). This contradicts Haughton's (1930) statement that the forearm is relatively shorter in *Hovasaurus*. It should be remembered that his statement is true for immature specimens, and he did not have a complete growth series available to him.

The tibia is 85 per cent the length of the femur in *Tangasaurus* and *Hovasaurus* at maturity, and 90 per cent in '*Datheosaurus*'.

Many eosuchians, including *Youngina* (Broom 1922), *Tangasaurus* (Fig. 1), *Hovasaurus* (Piveteau 1926), '*Datheosaurus*' (Piveteau 1926) and *Kenyasaurus* (Harris & Carroll 1977), have ossified sterna. The dimensions and outline of the sternum of *Tangasaurus* fall within the range of *Hovasaurus*.

The coracoids of *Tangasaurus* and *Hovasaurus* are similar in outline. Haughton (1930) stated that they are distinguishable on the basis of proportions, but the coracoids of the type specimen of *Tangasaurus mennelli* are too poorly preserved to confirm this statement.

The humeri of *Tangasaurus* are identical in outline to those of many specimens of *Hovasaurus*. Well-ossified humeri of *Tangasaurus*, *Hovasaurus*, and '*Datheosaurus*' share the distinctive feature of a greatly expanded entepicondyle (Figs. 1–2). The width of the distal end of the humerus is up to 40 per cent of its length. It is worth noting that the known humeri of *Youngina* are all from immature animals and consequently do not show a well-ossified entepicondyle. However, the curvature at the base of the entepicondyle and the position of the entepicondylar foramen suggest that the humerus of mature individuals of *Youngina* also had a greatly expanded entepicondyle.

The tarsus of *Tangasaurus*, *Hovasaurus*, *Kenyasaurus*, and '*Datheosaurus*' is specialized in the loss of the fifth distal tarsal as a discrete element. Harris & Carroll (1977) refer to a specimen of *Hovasaurus* (MNHN 1908–21–10) and suggest that the fifth and fourth distal tarsals fuse at maturity.

A very distinctive characteristic of most specimens of *Hovasaurus* is the presence of abundant pebbles, mainly quartz, in the abdominal cavity (Fig. 2). It was assumed (Haughton 1930) that these were gastroliths, but they seem to be too numerous, large, and closely packed to have functioned effectively in food breakdown. Considering the apparent aquatic habits of *Hovasaurus*, it may be more appropriate to consider them as having served as ballast. The same function appears to be true for 'gastroliths' of crocodiles (Cott 1961) and plesiosaurs (Darby & Ojackangas 1980). Stomach stones are found in at least one specimen of '*Datheosaurus*' (MNHN 1908–11–5), (Piveteau 1926, pl. 11) but are few in number and possibly did serve as aids to digestion. When present, the relative abundance of stomach stones is a quick way to distinguish *Hovasaurus* from '*Datheosaurus*'. Absence of stomach stones from the *Tangasaurus* specimens does not necessarily mean that this genus did not swallow pebbles. Some

specimens of *Hovasaurus* do not have stones in the abdomen, so this may possibly be explained as post-mortem rupture of the abdominal cavity before the cadaver came to rest and was buried by sediment.

### TAXONOMY

In the light of improved knowledge of the morphology of the tangasaurids, it is possible to establish a diagnosis for the family. The relationship of the Tangasauridae to *Youngina* will be considered here as well.

In recent years, it has become widely accepted that a proper taxonomic diagnosis should emphasize derived (advanced) character states rather than the retention of primitive characters. Characters listed in the following suprageneric diagnoses are derived and can be used to distinguish the taxa from all known eosuchian taxa that are not considered in this paper. Numbers in parentheses refer to Figure 6.

Class REPTILIA Linnaeus, 1758

Subclass LEPIDOSAURIA Duméril & Bibron, 1839

Order EOSUCHIA Broom, 1914

Suborder YOUNGINIFORMES Romer, 1945

Superfamily YOUNGINOIDEA superfam. nov.

Fig. 6

#### *Diagnosis*

Distinctive sutures on parietal for frontal and postfrontal (1). Accessory intervertebral articulation present on mid-line of dorsal neural spine (2). Co-ossification of paired sternal plates into a single unit in mature animals (3). Entepicondyle of humerus strongly developed at maturity (4). Olecranon process and sigmoidal notch of ulna poorly developed in mature animals (5); radius longer than shaft of ulna (6).

Family **Younginidae** Broom, 1914

*Youngina* Broom, 1914

#### *Diagnosis*

3 premaxillary, 15–23 maxillary, and 20 dentary teeth. Zygapophyses of anterior dorsal vertebrae extend laterally beyond the centra and inclined at low angle from horizontal; neural spines low and rectangular. Iliac blade short and almost vertical. Humerus only about 70% length of femur, compared with 75% in immature *Hovasaurus* and 110% in mature *Hovasaurus*. Radius 80% length of humerus, and 60% length of tibia; tibia 90% length of femur. Proximal head of fifth metatarsal expanded but not hooked.



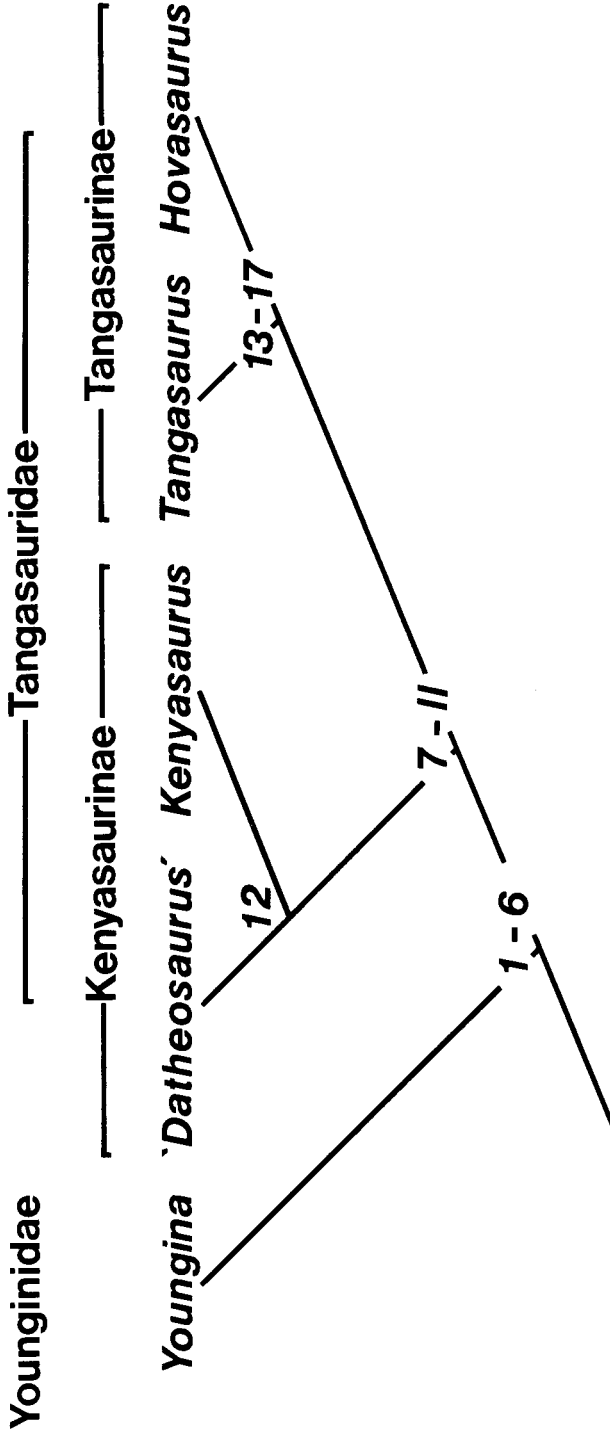


Fig. 6. Phylogenetic chart showing the apparent interrelationships of younginoid eosuchians. Numbers refer to characters discussed in the text.

Family **Tangasauridae** Camp, 1945*Diagnosis*

Humerus as long as or longer than femur in mature animals (7); radius 50–65 per cent length of humerus and 65–75 per cent length of tibia at maturity. Scapula low in lateral aspect and mainly a ventral element (8); coracoid as large as the scapula (9). Medial centrale contacts fourth distal carpal, thereby preventing contact between the lateral centrale and third distal carpal (10). Fifth distal tarsal not a discrete element (11).

Subfamily **Kenyasaurinae** subfam. nov.*Diagnosis*

19–28 pairs of caudal ribs and transverse processes present, all of which taper distally (12).

*Kenyasaurus* Harris & Carroll, 1977*Type species*

*Kenyasaurus mariakaniensis* Harris & Carroll 1977: 140.

*Diagnosis*

Low but anteroposteriorly elongate neural spines in the dorsal region; 56 caudal vertebrae; 28 pairs of caudal ribs and transverse processes. Astragalus almost triangular rather than primitive L-shape; pronounced process on fifth metatarsal for insertion of peroneus brevis.

*Thadeosaurus colcanapi* Carroll, 1981

*Broomia madagascariensis* Piveteau, 1925: 157.

*Datheosaurus* sp., Piveteau, 1926: pl. 17 (fig. 2).

*Tangasaurus menelli*, Piveteau, 1926: pl. 10 (figs 1–2), pl. 11 (figs 1–2), pl. 12 (fig. 1), pl. 16 (fig. 2).

*Diagnosis*

Neural spines tall and rectangular in dorsal region; 47 caudal vertebrae; 19 pairs of caudal ribs and transverse processes. Small numbers of gastroliths present in abdominal cavities of some specimens.

Subfamily **Tangasaurinae** Piveteau, 1926*Diagnosis*

Neural spines high in dorsal region and higher in proximal and mid-caudal regions (13). 9–12 pairs of caudal ribs (14); anterior caudal ribs expanded distally (15); haemal spines large and platelike (16). Presacral intercentra, with the exception of the first three, do not ossify until animal is mature (17).

*Tangasaurus* Haughton, 1924*Type species*

*Tangasaurus mennelli* Haughton, 1924: 3.

*Tangasaurus* Piveteau, 1925: 155.

*Tangasaurus menelli* Piveteau, 1926: 78.

*Tangasaurus minelli* Peyer, 1937: 115.

*Diagnosis*

Neural spines of dorsal vertebrae high and rectangular; height of neural spine of mid-caudal vertebra about 35 per cent greater than length of associated centrum, and about 75 per cent length of associated haemal arch and spine.

*Hovasaurus* Piveteau, 1926*Type species*

*Hovasaurus boulei* Piveteau, 1926: 78.

*Diagnosis*

Skull lacks tabular. 5 cervical, 20 dorsal, 2 sacral and at least 70 caudal vertebrae. Height of neural spines of mid-dorsal vertebrae at least 75 per cent greater than length of associated centrum, whereas height of a mid-caudal neural spine can be more than 125 per cent greater than length of associated centrum; neural spine of mid-caudal vertebra almost 90 per cent length of associated haemal arch and spine. Mammillary processes on neural spines of anterior dorsals. Ribs slightly pachyostotic in mature animals. High number of stones in abdominal cavity suggesting they were used as ballast.

## CONCLUSIONS

*Tangasaurus mennelli* is represented only by three specimens from the Tanga region of Tanzania. Specimens from Madagascar that have been attributed to this species represent a distinct as-yet-unnamed genus that Piveteau (1926) referred to as '*Datheosaurus*' and that is being described by Carroll (1981).

Four genera from Africa and Madagascar are herein assigned to the Tangasauridae. Two subfamilies are recognized on the basis of differences in caudal anatomy. Kenyasaurines were not as highly specialized for an aquatic existence as were the tangasaurines and they were intermediate in morphological specialization between *Youngina* and *Hovasaurus*. Tangasaurids and younginids share a number of derived characters and, therefore, have been united into a single superfamily, the Younginoidea.

*Acerosodontosaurus* (Currie 1980), *Galesphyrus* (Carroll 1976a), and *Heleosaurus* (Carroll 1976a) have recently been referred to the Younginidae, but they do not possess the derived characters shared by *Youngina* and the tangasaurids. Therefore, they should not be considered as younginoids. Their systematic position will be considered in a separate paper.

The shared derived characters of the Younginoidea are not found as a suite in other eosuchians, which strongly suggests that *Youngina* is not the ancestral morphotype for any eosuchians other than the Tangasauridae.

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